

THE PHYLOGENY OF THE GLYPTOSTERNOID FISHES (TELEOSTEI: SILURIFORMES, SISORIDAE)

by

Shunping HE (1) (2)

ABSTRACT. - The glyptosternoid fishes are freshwater catfishes belonging to the family Sisoridae. There are 9 genera containing 28 species in glyptosternoid fishes. This group can be identified from other sisorid fishes by the following main three characters: the last unbranched pectoral fin ray bearing many pointed protrusions which are unmineralized bony structure along the anterior margin which are enveloped in the skin; the lack of an adhesive organ on the breast; and the horizontal insertion of the pectoral and ventral fins. These characters appear to be adaptations to the fast running brooks at high altitudes or at the base of the hills, where most of these catfish are found. The phylogenetic analysis based on 60 osteological characters was run with the Hennig 86 program; only one cladogram was produced. The following relationships of glyptosternoid fishes are hypothesized: (1) The glyptosternoid fishes form a monophyletic group which is defined by 13 apomorphies; (2) Among glyptosternoids *Glyptosternum* is the most primitive genus; it bears many plesiomorphies; (3) Some external characters are interpreted as ecological adaption result. They are incongruent with the evolutionary polarity stemmed from the osteology. Examples are the posterior labial fold and the mouth sucker, these had have been treated as the systematic characters and used to produced evolutionary tree; (4) Many of the characters which occur in a group of taxa including *Exostoma*, *Glaridoglanis*, *Pseudexostoma* and *Oreoglanis* which appears to have gained a number of derived features by convergence. But the character analysis indicated that some specialized characters of the *Exostoma* and *Glaridoglanis* are derived directly from the primitive state, they have not systematic relationships with the *Pseudexostoma* and *Oreoglanis* (having the mouth sucker, continuous labial fold); (5) The genus *Pareuchiloglanis* is not monophyletic; it forms a monophyly only with *Pseudexostoma* and *Oreoglanis*.

RÉSUMÉ. - Les glyptosternoides sont des poissons-chats d'eau douce de la famille des Sisoridae. Ce groupe est constitué de 9 genres et 28 espèces et peut être différencié des autres Sisoridae par les trois caractères suivants: dernier rayon épineux non branchu des nageoires pectorales mou et segmenté, chaque segment portant une expansion plus ou moins longue en avant de son bord antérieur; absence d'appareil adhésif sur la face ventrale et insertion ventrale des nageoires pectorales et pelviennes. Ces caractères apparaissent comme des adaptations aux courants torrentiels de haute altitude ou de la base des montagnes. Une matrice de 60 caractères ostéologiques, traitée par le programme "Hennig 86", donne seulement un cladogramme avec lequel nous avons fait l'hypothèse phylogénétique ci-dessous: 1) Les poissons glyptosternoides forment un groupe monophylétique défini par 13 apomorphies; 2) *Glyptosternum*, qui porte de nombreuses plesiomorphies, est le genre le plus primitif; 3) Quelques caractères externes sont adaptatifs en liaison avec l'écologie. Aussi sont-ils non congruents avec la polarité des caractères ostéologiques. C'est le cas du repli labial postérieur et de la ventouse buccale, mais ils ont été traités comme des caractères systématiques et utilisés pour produire des arbres phylogénétiques; 4) Des caractères conflictuels sont présents dans un ensemble regroupant *Exostoma*, *Glaridoglanis*, *Pseudexostoma* et *Oreoglanis* qui ont acquis un certain nombre de caractères spécialisés par convergence. Mais l'analyse montre que quelques caractères des genres *Exostoma* et *Glaridoglanis* dérivent directement d'un état primitif; ils n'ont pas de relation de parenté avec *Pseudexostoma* et

(1) Institute of Hydrobiology, CAS, Wuhan, Hubei 430072, P.R. CHINA.

(2) Laboratoire d'Ictyologie générale et appliquée, Muséum national d'Histoire naturelle, 43 rue Cuvier, 75231 Paris Cedex 05, FRANCE.

Oreoglanis (qui ont une ventouse orale et un repli labial continu); 5) *Pareuchiloglanis* n'est pas un groupe monophylétique. Ce genre forme un ensemble monophylétique quand on l'associe avec les genres *Pseudexostoma* et *Oreoglanis*.

Key-words. - Siluriformes, Glyptosternoid, Sisoridae, Phylogenetic relationships.

The glyptosternoid fishes are freshwater catfishes belonging to the family Sisoridae. This group can be identified from other sisorid fishes by the following main characters (Hora, 1952): 1. the unbranched pectoral fin ray soft, giving off many pointed protrusion which is unmineralized bony structure (or soft pointed cartilaginous rays) along the anterior margin which are enveloped in the skin of the fin; 2. the lack of an adhesive organ on the breast; and 3. the horizontal insertion of the pectoral and ventral fins. These characters appear to be adaptations to the fast running brooks at high altitudes or at the base of the hills, where most of these catfish are found (Chu, 1979).

Most of glyptosternoid species were named in the present century, but some descriptions were made in the nineteenth century. McClelland (1842) was the first to describe the group when he erected the genus *Glyptosternum* and the new species *G. reticulatum* from India. By 1952, two more species were included in this genus: first the Tibetan species, *Paraexostoma maculatumand*, described by Regan (1905) was rearranged in this genus as *G. maculatumand* by Hora (1923); second, Hora and Silas (1952) published the Afghan species *G. akhtari*. Blyth (1860) erected a new genus, *Exostoma* for the Burma species, *E. berdmorei*. Following this, *E. labiatum* (McClelland) 1842 and *E. vinciguerrae* (Regan) 1905 were included in this genus. In 1907, Regan considered *Chimarrichthys davidi* (Sauvage), which was found in the Chinese province of Sichuan, as the type species of the new genus, *Euchiloglanis*. Kimura (1943) described *E. kishinouyei* from Sichuan as a member of this genus. After, this species had been arranged in genus *Coraglanis* for very long time and until 1981 it was rearranged in *Euchiloglanis* by Chu. Norman (1925) established the new genus *Glaridoglanis* with *Exostoma andersonii* (Day) as type species and the only member. Smith (1933) erected a new genus, *Oreoglanis*, with his description of *O. siamensis* from Thailand, later arranging in this genus other species found in China and Burma, *O. macropterus* (Vinciguerra) and *O. delacouri* (Pellegrin). In 1936, Pellegrin erected the genus *Pareuchiloglanis* for a newly described fish species, *P. poilanei*, from Vietnam. From 1936 to 1981, no new species were described for *Pareuchiloglanis*. Chu (1981) considered that most species of the genus *Euchiloglanis* must be arranged within *Pareuchiloglanis*, on the basis of the description of type species the *Euchiloglanis* in which the tooth band of the upper jaw stretches to each end of the jaw. This arrangement is referred to as the *Glyptosternum*-type in contrast to the *Pareuchiloglanis*-type in which the upper jaw tooth band is very narrow. Accordingly, seven species of the genus *Euchiloglanis* were arranged in the genus *Pareuchiloglanis* (with narrow tooth band), with the new species published later (Ding *et al.*, 1991; Fang and Cui, 1984; Wu and Chen, 1979; Yue, 1981), the 12 species were arranged in the genus *Pareuchiloglanis*.

In 1952, Hora and Silas erected the genus *Myersglanis*, with only one species, *M. blythi* (Day). Later Chu (1979) erected the genus *Pseudexostoma*, the type species of which is the Chinese *Glyptosternum yunnanensis* (Tchang), and included also the description of a Chinese subspecies, *P. yunnanensis brachysoma*. Finally, Wu and He (1981) established the monotypic genus *Parachiloglanis*, taking *Glyptosternum hodgarti* (Hora) as the type and accounting for the ninth of nine genera containing 28 species of glyptosternoid fishes.

Glyptosternoid fishes are mainly distributed in the water systems of the Qinghai-Tibet highland and the Huenduan mountains (the eastern part of this plateau). It can also be found, outside China, in Indian, Nepal, Vietnam, Burma, Bangladesh, Thailand, etc. The main basins in which these fishes live are: Yaluzhangbu (Tsaopo), Irrawaddy, Nujiang (Salween), Nanchangjiang (Mekong), Jingshajiang (Upper streams of the Yangtze River), Yuangjiang (Red River), Nanpanjiang (upper streams of the Pearl River), and Brahmaputra basin. Some species can distribute as far as the River Indus and River Kabul. Hora (1952) first described the geographical distribution of glyptosternoids in a paper dealing with glyptosternoid systematics, based on adaptive structures such as the maxillary barbels, pectoral fins, adhesive organs, and lower labial-folds. His conclusion suggested that *Glyptosternum* is the most primitive genus in the group, with all other genera developing from it, and its direct ancestor being *Glyptothorax*.

Hor (1952) considered that the original home of the glyptosternoids was the Chinese province of Yunnan and that the various genera and species of the group originated in a series of waves corresponding to intervals of tectonic movements in this region. In this way *Glyptothorax* became more and more specialized with the orogenic movement of the Himalayas. Similar work was done by Chu (1979), in which the analysis was based on adaptive structures. He also proposed *Glyptosternum* as the most primitive, and he divided the group into two branches: the first, containing *Glyptosternum*-like genera, in which the lower labial-fold is interrupted; and the second with *Exostoma*-like genera whose lower labial-fold is continuous, with the lips reflected and spread to form a broad flat sucker. Chu (1979) made no mention of Tilak's work (1963b) whose comparative research about the Sisoridae, indicated that some characters of the skull and Weberian apparatus are useful for phylogenetic and taxonomic interpretations. The glyptosternoid fishes form a natural group, as defined by Hor (1952), whose special distribution is meaningful in considering the biogeographical development of the Himalayan region. In particular, his phylogenetic interpretation is helpful in determining the development of water systems in the area. At present time, there is no comprehensive systematic research for the glyptosternoid fishes. Their definition and cladogram, based on their osteology, have not been decided. This study is an attempt to resolve the taxonomic and systematic confusion concerning the glyptosternoid fishes.

MATERIAL AND METHODS

The material for the anatomical study was provided mainly from collections at the Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan (IHCAS). Other major collections extensively examined include those in the Museum national d'Histoire naturelle (MNHN) in Paris. Specimens for osteological studies were prepared using a technique modified after Dingerkus and Uhler (1977). The osteological observations and the figures were made on cleared and stained specimens, using a binocular microscope equipped with a drawing attachment.

Specimens examined

The in-group includes the following species:

Glyptosternum maculatum (Tibet) IZSX; *Euchiloglanis kishinouyei* (Sichuan) IHCAS; *E. davidi* (Sichuan) IHCAS; *Pareuchiloglanis feae* (Yunnan) IHCAS; *P. kamengensis* (Yunnan) IHCAS; *P. gongshsanensis* (Yunnan) IHCAS; *P. sinensis* (Sichuan) IHCAS;

P. anteanalis (Sichuan) IHCAS; *P. sichuanensis* (Sichuan) IHCAS; *P. robusta* (Sichuan) IHCAS; *P. poilanei* (Vietnam) MNHN 1936-19 and 20 (Types); *P. macrotrema* (Tonkin Chevey) MNHN 1935-352; *P. longicauda* (Guizhou) IHCAS; *P. myzostoma* (Yunnan) IHCAS; *P. gracilicaudata* (Yunnan) IHCAS; *Pseudexostoma labatum* (Tibet) IHCAS; *Glari-doglanis andersoni* (Tibet) IHCAS; *Exostoma labiatum* (Mts. Cavein) MNHN 1893-142 et 143; *Exostoma labiatum* (Tibet) IHCAS; *Oreoglanis macropterus* (Yunnan) IHCAS.

The out-group includes the following sisorid species:

Bagarius bagarius (Yunnan) IHCAS; *B. bagarius* (Cambodge) MNHN 1967-470 to 472; *B. yarrelli* (Yunnan) IHCAS; *B. yarrelli* (Tonkin, now Vietnam) MNHN 1934-286 to 290; *Pseudecheneis sulcatus* (Yunnan) IHCAS; *Glyptothorax fukiensis* (Sichuan) IHCAS; *Glyptothorax majus* (Borneo) MNHN 1891-484 to 487.

The cladogram was produced using a computer-based character analysis. The method of the out-group comparison was used to decide the evolutionary polarity of the characters. The out-groups used are the two widely distributed genera belonging to the Sisoridae, *Bagarius* and *Glyptothorax*. The Diplomystidae have been traditionally regarded as the most primitive taxon of the Siluroidei (Regan, 1911; Alexander, 1965; Chardon, 1968; Lundberg and Baskin, 1969; Fink and Fink, 1981; Arratia, 1987), so Diplomystidae are treated as the reference here for deciding the evolutionary polarity, the characters of this family here has been obtained mainly from Arratia (1987) and Alexander (1965).

The software Hennig 86 employed in the phylogenetic analysis, stems from the cladistic methodology founded by Hennig (1966) and developed by many subsequent authors.

OSTEOLOGY OF *GLYPTOSTERNUM MACULATUM* (REGAN) 1905

Neurocranium (Figs 1, 2, 3)

The neurocranium has the shape of a triangular, rostral taper wedge. It is considerably broadened posteriorly and narrow anteriorly. The bones of the dorsal surface form a strong cranial roof. There is a long, narrow anterior and a short, narrow posterior fontanelle on the cranial roof. The cranium is shallow excavated posteriorly and furnished with a broad occipital and two lateral processes of the posttemporal. The complex vertebra is intimately associated with the hind end of the basioccipital and the exoccipitals.

Ethmoid (Figs 1, 2, 3, eth). - The ethmoid is a prominent bone in the cranium; it forms the most anterior part of the neurocranium and is a greatly depressed, T-shaped bone. Its anterior end is slightly notched and is produced into two ethmoidal cornua to which the premaxillae are attached. The bone is cleft behind and constitutes the anterior boundary of the anterior fontanelle; the ethmoid is excavated ventrally to suture with the arrow-head of the vomer.

Lateral ethmoid (Figs 1, 2, 3, leth). - The lateral ethmoid is an elongate, irregular shaped-bone which form a narrow area of dorsolateral surface of the cranium. It is produced laterally into a prominent head and posteriorly into a long thin process, which runs outside the frontal and interdigitates with it. The head bears, at its distal end, an articular facet for the autopalatine and has a foramen in front for the exit of ophthalmicus superficialis of the fifth and seventh cranial nerves.

Vomer (Figs 2, 3, vo). - This vomer is arrow-shaped redundant, its posterior process tapers caudad in a groove in the parasphenoid. The two lateral vomerine proc-

esses on its head suture with the lateral ethmoids. The vomer lies horizontally underneath the ethmoidal region and firmly suturing the ventral surfaces of the ethmoid, lateral ethmoids, and parasphenoid.

Frontal (Figs 1, 3 fr). - The paired frontal are large, elongate bony plates roofing the area between the ethmoidal and post cranial regions. They suture anteriorly with the ethmoid and lateral ethmoids, ventrally with the orbitosphenoids and pterosphenoids and posteriorly with the suproccipital and sphenotics. The two frontals are largely separated by the two well-developed anterior and posterior fontanelles, and only suture with each other medially halfway along their length *via* a bony bridge which separates the anterior fontanelle from the posterior.

Sphenotic (Figs 1, 2, 3, sph). - The sphenotic is a relatively small bone placed lateral to frontal and supraoccipital. It is sutured with frontal, pterotic, prootic, and also the supraoccipital. The sphenotic bears a main portion of the crescentic fossa for the hyomandibular.

Pterotic (Figs 1, 2, 3, pto). - The pterotic is a relatively large bone, which forms the main part of the posterior cranium. On the cranial roof the pterotic sutures with the sphenotic anteriorly, supraoccipital medially and posttemporal posteriorly. On the ventral face of the cranium, the pterotic sutures with the prootic, sphenotic, exoccipitals, and posttemporal.

Supraoccipital (Figs 1, 3, 4, suo). - The supraoccipital forms the posteromedian roof of the skull. Anteriorly it is contacted by the frontals, laterally by the sphenotics, pterotics, and posttemporals. Anteromedially the supraoccipital bears a deep notch which forms posterior part of the posterior fontanelle. Posteriorly, the bone is produced into a short, little broad supraoccipital process. This process, with its posterior end, contacts the neural spine of the complex vertebra through a suture.

Parasphenoid (Figs 2, 3, psh). - The single parasphenoid forms the ventral keel of the neurocranium, its body is produced laterally into wings. The stem of the bone is straight; in front and behind, the body has jagged interdigitating sutures with the ethmoid and basioccipital, respectively. It also articulates with the vomer, lateral ethmoids, orbitosphenoid, pterosphenoids, and prootics.

Orbitosphenoid (Figs 2, 3, ors). - The orbitosphenoid is a tubular elongated bone partially open dorsally. It holds the olfactory tracts in a large channel and separates the two orbits by its lateral rim. Anterolaterally the bone joins the lateral ethmoid both synchondrally and with a very strong interdigital suture at each side; the dorsal edges of its lateral walls suture to the ventral surface of the frontals. Posteroventrally the orbitosphenoid overlies and is firmly sutured to the anterior part of the parasphenoid ventrally. Posteriorly, the orbitosphenoid joins the pterosphenoids synchondrally with suture.

Pterosphenoid (Figs 2, 3, pts). - The pterosphenoid is an irregular-shaped bone situated on either side of the parasphenoid. The anterior and median parts contribute to the optic foramen and the median as well as the posterior to the trigeminofacial fenestra.

Prootic (Figs 2, 3, pro). - The prootic is a thin bony plate, situated dorsally on each side of the posterior part of the parasphenoid. The prootic also sutures with the pterotic, pterosphenoid, and exoccipital. It is notched in front for the exit of the trigeminofacial complex nerve.

Basioccipital (Figs 2, 3, 4, bo). - The basioccipital is an elongate bone with two posterolateral processes. This bone interdigitates anteriorly with the parasphenoid, while it forms a concave centrum-like condyle for the articulation with the first centrum posteriorly. On each side, an exoccipital articulates with the basioccipital.

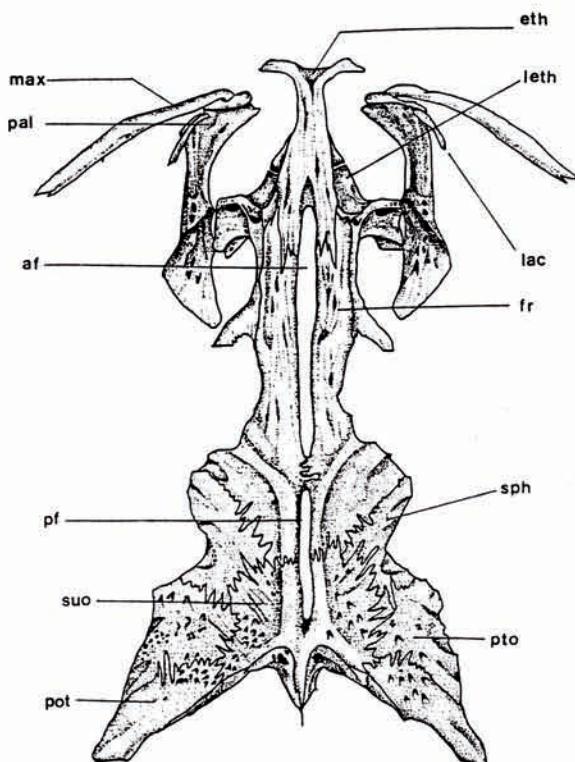


Fig. 1. - *Glyptosternum maculatum*. Cranium in dorsal view.

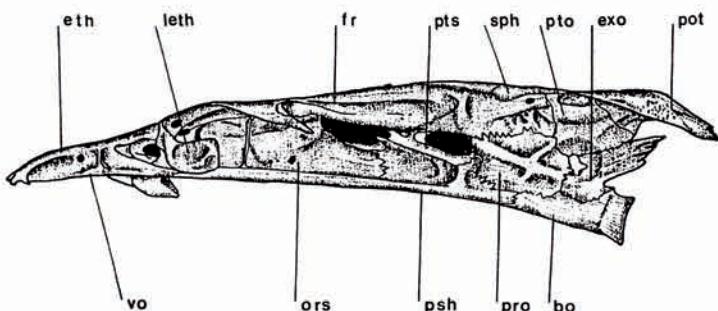


Fig. 3. - *Glyptosternum maculatum*. Cranium in lateral view.

Exoccipitals (Figs 2, 3, 4, exo). - The exoccipitals are a pair of irregular bones with their inner side attaching the basioccipital. They also suture with prootic and pterotic by its anteriorolateral side. Posteriorly, there is a process which gets contact to the gasbladder capsule of the complex vertebra, dorsally.

Epioccipitals (Fig. 4, epo = epiotic). - The epioccipitals are small bones situated on the lateral corner of the posterior wall of the neurocranium. They are discernible

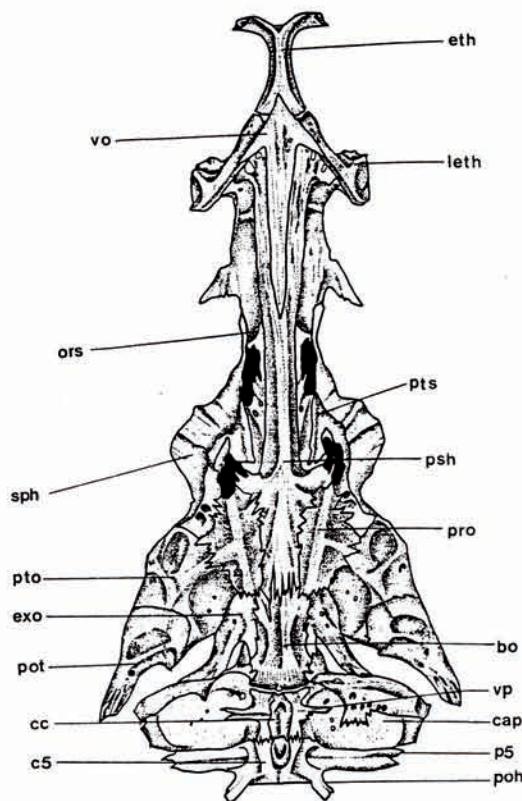


Fig. 2. - *Glyptosternum maculatum*. Cranium and complex vertebra in ventral view.

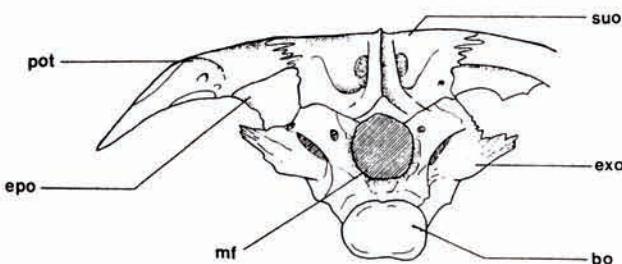


Fig. 4. - *Glyptosternum maculatum*. Cranium in posterior view.

only as a projecting shelf from the posterior side of conical in shape and produced posteriorly into blunt spine.

Nasal bones

The nasal bone is tube-like and buried in the soft tissues of the ethmoid region, lying along each side of the ethmoid, it does not contact other bones.

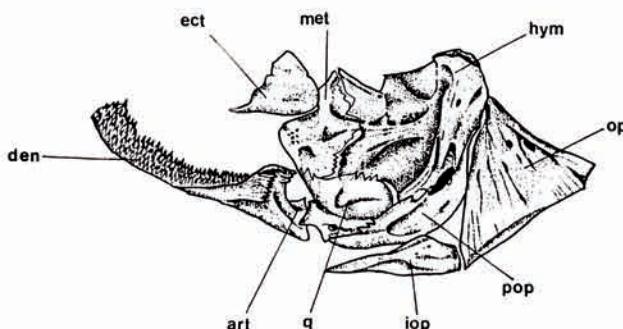


Fig. 5. - *Glyptosternum maculatum*. Suspensorium and mandible in lateral view.

Infraorbitals

The infraorbital series comprise several very small bones partially surrounding the orbit. The first one the lachrymal (Fig. 1, lac) is a thin, long bar, arch-like with its posterior end notched. It is situated anterolateral to the autopalatine, contacting the autopalatine and maxilla by the ligament. The other infraorbitals are all tube-like, becoming the infraorbital canal.

Jaws and suspensorium

Premaxillary. - The premaxillaries are plate like and bear villiform teeth. The tooth band on each premaxilla is broad and on the sides it bends posteriorly into tapering end. It attaches to the ethmoidal cornua via massive connective and ligamentous tissues. On the dorsal surface, each plate bears a ridge, which provides an attaching surface for the ethmoid.

Maxilla (Fig. 1, max). - The maxilla is a mobile bony rod. It is grooved on its medial side to lodge the cartilage of the maxillary barbel. It lies on each side of the ethmoid dorsal to the premaxilla; it is well developed and tapers proximally and spatulates distally. With its base end, it connects to the palatine by the ligament.

Palatine (Fig. 1, pal). - The autopalatines are enormously developed. They are broad, strong and spatulated at both ends, articulating with the lateral ethmoid by its center, and posteriorly enclose a space in connection with the posterior process of the ethmoid (Tilak, 1963b considered that the process is an independent bone and named it the arch like bone AB). Its posterior extremity is much expanded and lies over the ectopterygoid.

Dentary (Fig. 5, den). - The dentaries are stout, elongated, and curved. The anterior two thirds of their surface is very broad and surrounded with small villiform teeth. Their posteromedial margin is grooved for the Meckel's cartilage. Posteriorly, the dentary forms a prominent ridge.

Articular (Fig. 5, art). - The articular is a very small bone situated on the posterior end of the dentary. It is a triangular bone articulated with the quadrate.

Hyomandibular (Fig. 5, hym). - The hyomandibular is somewhat rectangular, articulating with the neurocranium via an elongate dorsal condyle accommodated in a long shallow hyomandibular fossa. The posteroventral margin of the hyomandibular firmly sutures with the preopercular and the anteroventral margin joins the quadrate synchronously. Its anterior margin joins the posterior margin of the metapterygoid; between

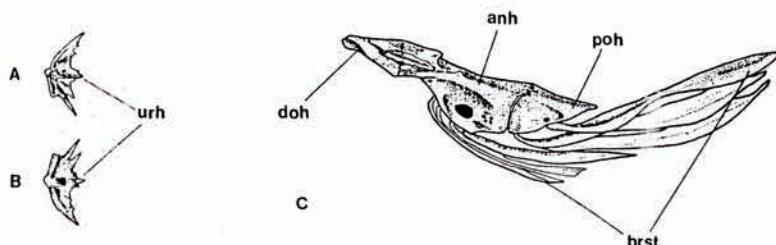


Fig. 6. - *Glyptosternum maculatum*. Hyoid branchial elements. A: urohyal in dorsal view; B: urohyal in ventral view; C: hyoid arch and branchiostegals in lateral view.

the quadrate and hyomandibular, there is a groove with cartilage on the posterior margin of the quadrate.

Quadrat (Fig. 5, q). - The quadrate has a condyle at its anterior end for the angular. Its lateral ventral margin firmly sutures with the first half part of the preopercular. Its dorsolateral margin sutures with the hyomandibular and the metapterygoid.

Ectopterygoid (Fig. 5, ect). - The ectopterygoid is a triangular thin, flat bone extending between the metapterygoid and autopatine. Its posterior tip connect loosely to the metapterygoid by a ligament and its anterior part overlaps the autopatine.

Metapterygoid (Fig. 5, met). - The metapterygoid is a large, thin bony plate lying anterodorsal to the quadrate and anteriorly to the hyomandibular. Its anterior margin attaches the ectopterygoid loosely by a ligament.

Opercular series

Opercular (Fig. 5, op). - The opercular is a large triangular bony plate linked to the hyomandibular at its dorsal apex *via* a condylar articulation. The anteroventral corner of the triangle is much extended, and its tip is contacted to the posterior margin of the interopercular. Its lateral surface is ornamented with numerous radiate ridges converging to the apex.

Interopercular (Fig. 5, iop). - The interopercular is an elongate, triangular flat bone situated anterior to the opercular and ventrolateral to the preopercular. Its posterior part is a little wide and its anterior part is tapered and extend as far as the anterior tip of the preopercular.

Preopercular (Fig. 5, pop). - The preopercular is an elongate bony plate lying along the posterior margins of both the hyomandibular and the quadrate and firmly sutured with both of them.

Hyoid arch (Fig. 6)

Anterohyal (Fig. 6-C, anh). - The anterohyal is the largest element in the hyoid arch. Its posterior half is enlarged as the fan-shaped and synchondrally joins the posterothyial with a prominent interdigital suture laterally; its anterior part is stout and cylindrical and joins the posterior end of the dorsohyal.

Dorsohyal (Fig. 6-C, doh). - The dorsohyal is a triangular bone with its posterior part joined to the anterohyal. Its anterior part is tapered and contacts its antimere by ligament.

Posterothyial (Fig. 6-C, poh). - The posterothyial is a compressed, triangular bony plate, which had its anterior edge synchondrally joining the anterohyal with suture

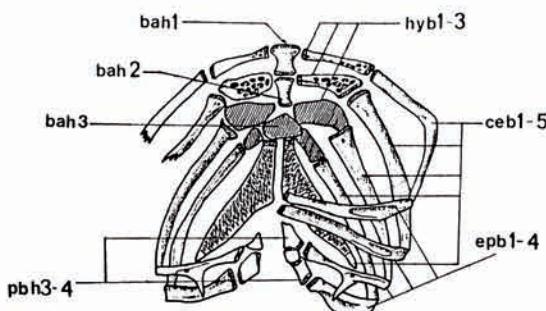


Fig. 7. - *Glyptosternum maculatum*. Branchial basket in dorsal view.

on lateral side. The posterior part is thick and is laterally attached to the interopercular by ligamentous tissue.

Interhyal (Fig. 6, inh). - The interhyal is a reduced, very small bone which is situated on the posterior apex of the posterohyal. Its tip attaching to the medial side of the hyomandibular and symplectic cartilage by ligamentous tissue.

Urohyal (Fig. 6-A,B, urh). - The urohyal is a single thin bone with several posterior processes. It lays medially behind the joint of the two dorsohyals. Seen ventrally, the bone is fan-shaped with two posterior lateral wings and one undeveloped posterior process. Its anterior head is thick and bears two stout lateral cornua which lodge in cavities of the dorsohyals. Dorsally the urohyal bears a thin laminar keel along its length, and anterodorsally the keel is modified into an elongate funnel-like structure.

Branchiostegal rays (Fig. 6-C, brst). - The branchiostegal ray series consists of seven elongate, arched bony rays with their dorsal end attaching to the ventral side of the anterohyal and posterohyal, four of which are on the anterohyal and the reminders on the posterohyal. The last three rays on the posterohyal are wider than that the other four, and they overlap each other to form a wholly plate.

Branchial arch (Fig. 7)

Pharyngobranchials (pbh1-4). - The pharyngobranchials consist of four elements on each side. The first and the second ones are reduced to a small stick-like bone tipped by cartilage at both ends and attached to the lateral side of the 1st and 2nd epibranchial individually, *via* membranous tissue along its length. The third one is ossified and is the largest in the series. It is triangular shaped. The anterior end of the bone is linked to the upper end of the 2nd epibranchial *via* cartilages and connective tissue, and the posterior end is firmly attached to the 4th pharyngobranchial and 3rd epibranchial. The fourth is a small bony plate linking the 3rd pharyngobranchial and fourth epibranchial. It broadly joins the upper pharyngeal tooth plate ventrally in a thick synchondrosis. The tooth plate is a small oval bony plate bearing numerous conical teeth on its ventral side.

Epibranchials (epb1-5). - The first four epibranchials are elongate bony beams with their lower ends, laterally directed, linking to the upper ends of the corresponding ceratobranchials. The first two have their upper ends linked together with the anterior end of the 3rd pharyngobranchial through connective tissue. The 3rd epibranchial has a long process extending over the 4th epibranchial midway. Upper end of the 3rd epibranchial is linked to the 3rd and 4th pharyngobranchials through connective tissue. The 4th epibranchial had its upper end linked to the upper pharyngeal tooth plate and 4th pharyngobranchial, and this element is a little wide. The 5th epibranchial is vestigial.

Ceratobranchials (cebl-5). - The ceratobranchials are the longest elements in the gill arches. The first four are long, arched bony beams. The 5th element is broadened, modified and bears numerous villiform teeth on its dorsal side.

Hypobranchials (hyb1-4). - There are only four pairs of separated hypobranchials. The first and the second hypobranchials are ossified, The first one is rod-like, and the second one is a fan-like bone. The third and the fourth hypobranchials are separate rectangle cartilaginous plates. The fourth one is smaller than the third one. I can not observe the separated 5th hypobranchial, but on the anterior end of the 5th ceratobranchial, there is a reduced cartilaginous tissue; may be it is the 5th hypobranchial.

Basibranchials (bah1-3). - The basibranchial series consists of two ossified rod-like bone and a thick cartilage. The first two basibranchials only connect to the correspondent hypobranchial, but the third basibranchial gets contact to the 3rd and 4th hypobranchials together; may be the separated 3rd basibranchial is a complex of 3rd, 4th and 5th basibranchials.

Complex vertebra and Weberian apparatus

Complex vertebra (Fig. 2). - The complex vertebra includes the first, second, third, and fourth vertebra. The first vertebra reduced very much to be a vestige, its appearance is a thin disk-like bony plate, without any paired processes borne on it. The 2nd-4th vertebrae are completely fused into a single unit, the complex vertebra (cc), and are indistinguishable as individual vertebra.

Dorsally, the complex vertebra bears the neural spinal, but the 1st neural spine can not be observed on my specimen, the most possible, it is reduced (in some primitive catfishes, there existed the vestige of the 1st neural spine, Mo, 1991). On the dorsal side of the complex vertebra, I can see only one thin bony plate, there is no fusc on this plate. So, I consider this is a complex neural spine (neural spine 2+3+4). The 5th neural spine is a distinguishable single bony plate, it is just behind the complex neural spine and contact it firmly by the fusc. The anterior margin of the complex attaches the posterior margin of the posterior process of the supraoccipital firmly by a suture.

Laterally, on the complex vertebra, there is a well developed parapophysis, which form a incomplete capsule (cap) open both ventrally and laterally. In most of the previous works, this structure is considered as the 4th parapophysis (Tilak, 1963b), the 2nd and 3rd parapophysis, being reduced. The gasbladder divided into two chambers and each situated in the incomplete capsule formed by the 4th parapophysis. The 5th parapophysis is modified when compared with the common vertebrae, its anterior margin is connected to the posterior margin of the 4th parapophysis firmly by the fusc.

Ventrally, on the middle of the complex vertebra, there existed a pair of ventral processes (vp), thin and long, independent, the free end a little enlarged, and attaches the ventral face of the gasbladder. Along the midline of the complex vertebra and the 5th vertebra, there is a wide groove, it is continuous from the complex vertebra and 5th vertebra. The post-haemalophysis (poh) of the 5th vertebra is a little more developed than that of common vertebrae. The 5th vertebra connects to the complex vertebra firmly by a suture.

Weberian apparatus. - In general, the Weberian apparatus comprises three units, tripus, scaphium and claustra, but same as in other sisoride fish, the claustra are apparently absent (Tilak, 1963b).

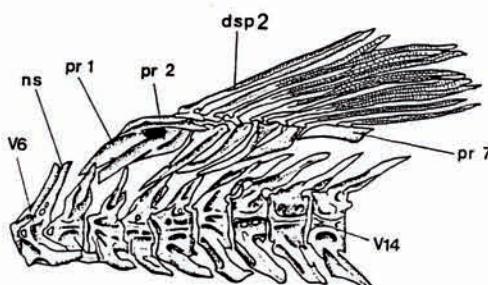


Fig. 8. - *Glyptosternum maculatum*. Vertebrae 6-14 in lateral view.

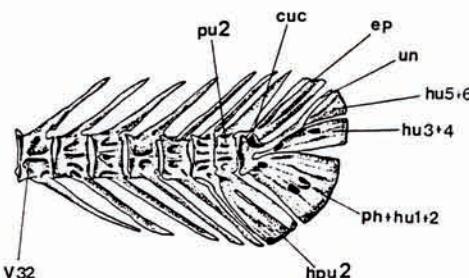


Fig. 9. - *Glyptosternum maculatum*. Caudal fin skeleton.

Vertebrae (Figs 8, 9)

The total vertebra count is 40 (including those 4 comprising the complex centrum and last fused urocentrum): 20 precaudal and 20 caudal vertebrae. The first four anterior have been described under the Weberian apparatus. The neural arches of the 6th to 11th vertebrae bear bifid neural spines. The remainder bear long slender neural spines. The neural arch of the 1st preural vertebra is a little shorter than those of the preceding vertebra. The 6th-20th vertebrae bear pleural ribs. The parapophysis of the vertebra preceding the 13th vertebrae are open, while those succeeding it are united into the haemal arches which have two well developed spines (incomplete arch?). In the caudal vertebrae, the haemal arches have only single spine.

Pectoral girdle and cranial linking bones

Posttemporal (Figs 1, 2, 3, pot). - The posttemporal is a large bone which sutures to the skull. Unlike most of other catfishes, the posttemporal does not have the inferior limb fused to the basioccipital. Its medial side is connected to the supraoccipital, and the anterior side is sutured to the pterotic. There is a strong ligament transverse from the posterior tip of the posttemporal to the outside of the capsule which is modified from the 4th parapophysis, this ligament is helpful to fix the upper tip of the cleithrum. Lundberg (1975) considers that most of the authors erroneously treated the supracleithrum as the posttemporal; the posttemporal is not the bone belonging to the skull but to the pectoral girdle, the evidence is that the sensory canal. The real posttemporal here is completely lost, this happened in many catfish family, such as Siluridae, Amblycipitidae, Sisoridae, etc.

Cleithrum (Fig. 10, ct). - The cleithrum forms most part of the pectoral girdle. It is larger than the coracoid and forms a major part of the girdle. It is a L-shaped stout bone with a very long posterior tip which is bifid, with which the cleithrum gets contact to the

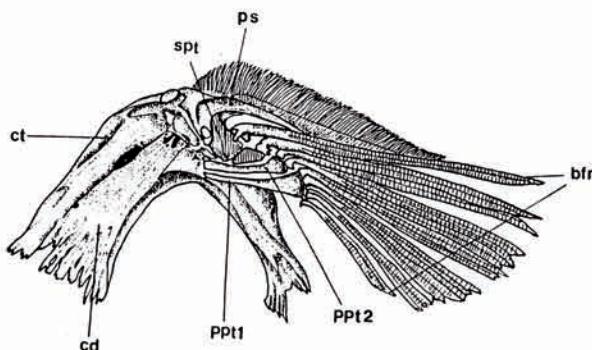


Fig. 10. - *Glyptosternum maculatum*. Pectoral girdle and fin skeleton.

skull by ligament. The horizontal portion is depressed and anteromedially directed and joining each other in a symphysis along the midline. The ascending portion is compressed, and is produced dorsally into a long tip which inserts into the groove between the posttemporal and the anterior margin of the capsule for the swimming bladder, and a blunt posterodorsal spine. The concave margin between the posterior tip and the blunt spine is spanned by massive connective tissue. The coracoid contacts to the cleithrum with the fuss along the medial of the two arms of the L-shape bone. On the out corner of the cleithrum, in the ventral margin, there is a small long facet for the head of the pectoral spine. This structure was not mentioned by Tilak in 1963a.

Coracoid (Fig. 10, cd). - The coracoid is narrower than the cleithrum and sutures to the inner side of the cleithrum. It is also a L-shaped bony plate, its horizontal portion is very depressed and anteromedially direct and joining each other in a symphysis along the midline. Between the cleithrum and the coracoid on the corner of the L-shaped bone, there is a hole. Dorsally the bone bears a keel-like lamina with its posterolateral part broadly suturing to the posteromedial side of the cleithrum. On the posterolateral end of the bone bears two condyles, the dorsolateral one has two articular facets, the outside one fits in a groove of the base of pectoral spine, the inner one only attaches the another articular surface of the pectoral spine; the small median one has a peg and articulates with a secondary cartilaginous radial. The humero-cubital process is not prominent.

Radial and fin rays (Fig. 10). - There are only two separate rod-like proximal radials (primary pterygials of Tilak, 1963a) (ppt) with their proximal end contacting on the coracoid, and its free ends are enlarged, fan-shaped, and articulate to the branched fin rays (bfr), the first proximal radial (ppt1) is connected to the third and fourth branched fin rays, and the second proximal radial (ppt2) is connected to the 5-11th branched fin rays. There is only one complex radial (secondary pterygials, Tilak, 1963a), it is a cartilage with two ossified areas for articular, there is an articular surface for the pectoral spine and another one for the coracoid, its dorsal surface is padded by the double head of 1st and 2nd branched fin rays. The fin rays include 11 branched fin rays, and a modified pectoral spine. The pectoral spine (ps) is rather soft and bears pinnate outgrowths on its outer border. Its head also, is double headed and has two articular facets to attach the coracoid, one of the articular facet is concave and connected with massive connective tissue. The cleithrum simply forms an articular facet for the head of the spine; thus there is no locking mechanism for the pectoral spine.



Fig. 11. - *Glyptosternum maculatum*. A: dorsal fin skeleton; B: skeleton of the first and second fin rays.

Dorsal fin skeleton (Figs 8, 11)

The dorsal fin is composed by seven elements, and each of them includes a proximal which is emerged in the body of the fish, connecting the fin ray to the neural spine of the vertebra, and a fin ray. The 1st and the 2nd are modified as a spine or reduced. The 1st and 2nd proximal (pr1, pr2) are modified also and fused to form a strong support for the dorsal spine. The 1st proximal is a long bony plate with a keel along its midline, its down extension wedging between the V-shaped neural spine of the 7th vertebra, also, they are fixed by strong connective tissues. The upper end of the 1st proximal is V-shaped and bifid, each of its posterior tip is fused with anterolateral tip of the 2nd proximal. The 2nd proximal also is a long triangular bony plate, along each side of its midline, there exists a keel, the anterior keel fuses to the posterior keel of the 1st proximal by the floss. Its down extension is tapered and contact with the first proximal firmly and they wedge into the V-shaped groove of the neural spine. Its upper end bears two wings on each side and a central protrude; the side wing has a anterior tip which fuses to the posterior tip of the 1st proximal. The central protrude has a anterior hook-like tip which locks the 2nd dorsal spine. The first dorsal spine is reduced and very difficult to find, it is a small triangle attaching on the second dorsal spine (dsp2). The second dorsal spine is the biggest dorsal fin ray whose anterior margin has the pinnate outgrowth; the head of the dorsal spine, at anterior view, is a fan-like stout bone, there is a hole on the center which hold the central protrude of the up end of the second proximal. At the posterior view, we can see two hook-like protrudes which attach the groove on second proximal.

The succeeding proximal radials are more or less uniform in shape and become progressively reduced in size. Their dorsal heads are turned backward and each articulates with a branched fin ray *via* a ball-like distal radial. Each branched fin ray is double headed and padded on the proximal radial.

Pelvic fin skeleton (Fig. 12)

The pelvic girdle consists of paired bony plates symphysial united along the midline. Each bone has two long anterior processes, a posterolateral condyle and an axe-shaped median portion. The median one (amp) of the two anterior processes has its lateral margin turned ventrally and its tip in contact with that of the counterpart bone, while the lateral one (alp) bears dorsally a long, laminar keel along its median margin. The posterolateral condyle has a crescentic articulatory surface with which articulate 6 fin rays. The first fin ray has modified just like that in the pectoral fin ray and is more stout than the fin ray posterior.

Anal fin skeleton (Fig. 13)

The anal fin skeleton is simply composed by the eight sets of proximal radials and branched fin rays. All the proximal radials (pr) are uniformed as the thin taper bony

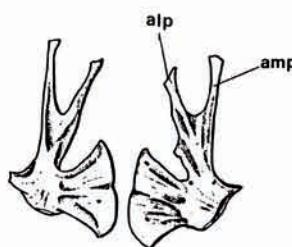
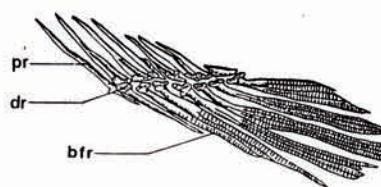
Fig. 12. - *Glyptosternum maculatum*. Pelvic girdle.Fig. 13. - *G. maculatum*. Anal fin skeleton.

plate except the last one, the last proximal radial is reduced as a small plate. All the branched fin rays (bfr) are double-headed and contact the proximal radial by the cartilage. But the first fin ray is unbranched, short and thinner than others.

Caudal skeleton (Fig. 9)

As in the other catfishes, the caudal skeleton is composed by two or three vertebrae, the first preural, the first ural and second ural. The compound ural centrum (cuc) is the main portion of the caudal skeleton and fused by the first preural and the first ural. The second ural is reduced to be a tube-like bone. It is very difficult to find it. On the anterior dorsal margin of the first preural, there is a pair of neural spines. The uroneural (un) is thin, long and taper; it is fused completely with the posterodorsal part of the compound centrum. A single, usually keeled, epural (ep) lies above the neural arch of the compound ural centrum. In the primitive catfishes, such as *Diplomystes* (Arratia, 1987) it bears six separate hypurals, but here, most of them are fused, also with the parahypural (ph), the fused pattern is: ph+hu1+hu2, hu3+hu4, hu5 (hu5+hu6 ?). On each side of the compound centrum a thin projection can be seen which is the reduced hypurapophysis.

RECOGNITION OF NATURAL GROUPS WITHIN GLYPTOSTERNOID FISHES

Glyptosternum McClelland 1842, contains 3 species: *G. reticulatum* McClelland 1842 (Indian), *G. maculatum* Regan 1905 (Tibet) and *G. akhtari* Silas 1952 (Afghan); there are many primitive characters in this genus, such as the gill opening extending to the ventral side, the less pectoral fin ray, also with its gasbladder bony capsule uncomplicated. The autapomorphies for this genus are: 1) the anterior tip of ethmoid is bifid with two long branches, and the tip notched deeply; 2) each premaxilla is composed by four bony plates; 3) there is a free hypural in the caudal skeleton.

Glaridoglanis Norman 1925, is monospecific: *G. andersonii* (Day 1869). The autapomorphy for this genus is: the teeth on the premaxilla are very strong, just like a chisel and their free end is blunt.

Exostoma Blyth 1860, contains 2 species: *E. labiatum* (McClelland 1842) and *E. vinciguerrae* Regan 1905, are so similar that sometimes they are considered as the same species (Wu and He, 1981). The autapomorphies for this genus are: 1) the shape of the premaxilla teeth is very complicate, its stem is very short, and its cap is long plate with a ridge (oar-like); 2) preopercular is especially developed; 3) the urohyal has not the posterior protrusion but only two postero-lateral processes.

Euchiloglanis Regan 1907, contains 2 species: *E. kishinouyei* (Kimura 1934) and *E. davidi* (Sauvage 1874), identifiable only on the measurement of the outer appearance. The autapomorphy for this genus is: each premaxilla is composed by three bony plates.

Myersglanis Hora & Silas 1952, is monospecific: *M. blythi* (Day 1869).

Oreoglanis Smith 1933, contains 3 species: *O. macropterus* (Vinciguerra 1890), *O. delacouri* (Pellegrin 1936) and *O. siamensis* 1933, that are similar to each other, only different in the measurements. The autapomorphy for this genus: the shovel-shaped premaxilla teeth only exist on the outer series of the lower jaw.

Pseudexostoma Chu 1979, is monospecific, but the single species is divided in two subspecies: *P. yunnanensis yunnanensis* (Tchang 1935) and *P. yunnanensis brachysoma* Chu 1979. The autapomorphy for this genus is: premaxilla teeth have two distinct types, those of the outer series on both jaws shovel-shaped and sparsely arranged in one or two rows, those of the inner side conical and numerous.

Parachiloglanis Wu 1980, is monospecific: *P. hodgarti* (Hora 1932). It is characterized by having no post-labial groove, the lower lip continuing with the isthmus without demarcation.

Pareuchiloglanis Pellegrin 1936, contains 12 species. Because some of the characters have been diversified, and it includes many species which are widely distributed, its monophyly is wanting careful consideration. In this genus, *P. sinensis* (Hora & Silas 1952), *P. robusta* Ding 1991, *P. anteanalis* Fang *et al.* 1984, *P. sichuanensis* Ding 1991 distribute in the same river system of Jinshajiang river; their morphological appearances and their osteological characters are similar, and they own some primitive characters. The *P. feae* (Vinciguerra 1890), *P. kamengensis* (Jayaram 1966), *P. gonshanensis* Chu 1979 all have the semi-free posterior labium, actually the primitive mouth sucker, so they form a specialized group; the *P. myzostoma* (Norman 1925), *P. gracilicaudata* Wu & Chen 1979, *P. longicauda* Yue, *P. macrostoma* (Norman 1925) and *P. poilanei* Pellegrin 1936 are between the two group above.

COMPARATIVE ANALYSIS OF THE CHARACTERS

Each genus is treated as a unit (OTU). But the genus *Pareuchiloglanis* includes 12 species, also is a composite assemblage of divergent forms, it is necessary to do the character analysis of this genus in order to decide its monophyly.

CS = character state, CS-0 = character state 0 and CS-1 = character state 1, etc.

1. The ethmoid and the formation of the anterior fontanelle: in *Diplomystes*, the posterior end of the ethmoid does not form the anterior margin of the anterior fontanelle, but it reaches the anterior tip of the anterior fontanelle (Alexander, 1965); same condition can be found in *Bagarius*. In *Glyptothorax*, it forms 1/3 first of the anterior fontanelle. In the glyptosternoid fishes, the length of the fontanelle marginated by the posterior fork of the ethmoid is different: *Glyptosternum* 1/3, *Glaridoglanis* 1/6, *Exostoma* 1/6, *Euchiloglanis* 1/6.5, *Pareuchiloglanis sinensis* 1/5, *P. anteanalis* 1/4, *P. myzostoma* 1/9, *P. longicaudata* 1/5, *P. macrostoma*, 1/7, *P. feae*, 1/5, *P. kamengensis* 1/11 and *Pseudexostoma* 1/10. Having shorter length of fontanelle marginated by the ethmoid is the plesiomorphic condition.

CS-0: the posterior end of the ethmoid does not or only forms 1/9, 1/10 and 1/11 of the anterior margin of the anterior fontanelle; CS-1: it forms 1/5, 1/6, 1/6.5 and 1/7 of

the anterior margin of the anterior fontanelle and CS-2: it forms 1/3 and 1/4 of anterior margin of the anterior fontanelle (Fig. 14, eth).

2. The anterior tip of ethmoid: in *Diplomystes*, the anterior tip of the ethmoid is bifid, its middle part is notched slightly, and in *Bagarius*, the anterior part of the ethmoid is T-shaped, with its anterior tip convex, this is an apomorphy. In *Glyptothorax*, the anterior part of the ethmoid is Y-shaped, bifid with its anterior tip notched. In the glyptosternoid fishes, most of the species have a shortly bifid, and slightly notched anterior tip. They are: *Euchiloglanis*, *Pareuchiloglanis sinensis*, *P. anteoanata*, *P. myzostoma*, *P. longicaudata*, *P. macrostoma*, *P. feae* and *P. kamengensis*; this character is similar to the primitive catfish *Diplomystes*; it is a plesiomorphy but in *Glaridoglanis*, *Exostoma* and *Pseudexostoma*, the anterior part of the ethmoid is very slightly notched and not bifid; this is an apomorphy. In *Glyptosternum*, the anterior tip bifid with two long branches, and the tip notched deeply is an apomorphy of this genus.

CS-0: the anterior tip of the ethmoid is shortly bifid and slightly notched; CS-1: it is very slightly notched and not bifid; CS-2: it is bifid with two long branches and the tip notched deeply; CS-3: it is T-shaped with its anterior tip convex (Fig. 14, eth).

3. The ratio of the length and width of the ethmoid: in *Diplomystes* and *Bagarius*, the width/length is about 1/1.5 and 1/1, in *Glyptothorax*, 1/3; in the glyptosternoid fishes this ratio is different: *Glyptosternum* 1/2.5, *Glaridoglanis* 1/4, *Exostoma* 1/4, *Euchiloglanis* 1/3.5, *Pareuchiloglanis sinensis* 1/5, *P. anteoanata* 1/4.5, *P. myzostoma* 1/5.3, *P. longicauda* 1/4.7, *P. macrostoma* 1/4, *P. feae* 1/4.5, *P. kamengensis* 1/5.5, *Pseudexostoma* 1/4. According to the concept of the out-group comparison, the evolutionary polarity is from short and wide ethmoid to the long and narrow one.

CS-0: the ratio of the length and width of the ethmoid is 1/1.5 or 1/1; CS-1: 1/2.5, 1/3, 1/3.5, 1/4, 1/4.5 and 1/4.7; CS-2: 1/5, 1/5.3 and 1/5.5 (Fig. 14, eth).

4. The lateral articular surface of the lateral ethmoid for the autopalatine: in *Diplomystes*, this surface is undeveloped (Arratia, 1987), its outer tip is taper and the surface for the autopalatine is very small. In *Bagarius*, the surface is a little developed, similar condition can be founded in *Glyptothorax*, but in the glyptosternoid fishes, this surface is very developed; the modified level of which in different species is various. The ratio of the width of the surface on the total length of lateral ethmoid is respectively, *Glyptosternum* 1/3 (Fig. 1), *Glaridoglanis* 1/2.8, *Exostoma* 1/3, *Euchiloglanis* 1/2.3, *Pareuchiloglanis sinensis* 1/3, *P. anteoanata* 1/2, *P. myzostoma* 1/2.5, *P. longicaudata* 1/2.8, *P. macrostoma* 1/2.5, *P. feae* 1/2.5, *P. kamengensis* 1/2.6, *Pseudexostoma* 1/2.5.

CS-0: this surface is little developed; CS-1: the ratio of the width of the surface on the total length of lateral ethmoid is 1/3 or 1/2.8; CS-2: 1/2.5 or 1/2.6; CS-3: 1/2.3 and 1/2 (Fig. 14, leth).

5. The posterior process of the lateral ethmoid: it is lacking in *Diplomystes*, but in *Bagarius* and *Glyptothorax*, it forms a narrow area on the cranium roof on each side. In the glyptosternoid fishes, the width of the posterior process of the lateral ethmoid is various; in *Glyptosternum*, *Exostoma*, *Euchiloglanis*, *Pareuchiloglanis sinensis* and *P. myzostoma*, it is a narrow and long strip, but in *Glaridoglanis*, *Pareuchiloglanis anteoanata*, *P. longicaudata*, *P. macrostoma*, *P. feae*, *P. kamengensis* and *Pseudexostoma*, this process is a wide strip, this last character is the apomorphic condition, because in the out groups the posterior process forms a very narrow strip on the cranium roof.

CS-0: the posterior process of the lateral ethmoid is lacking or forms a narrow area on the cranium; CS-1: it is a wide strip (Fig. 14, leth).

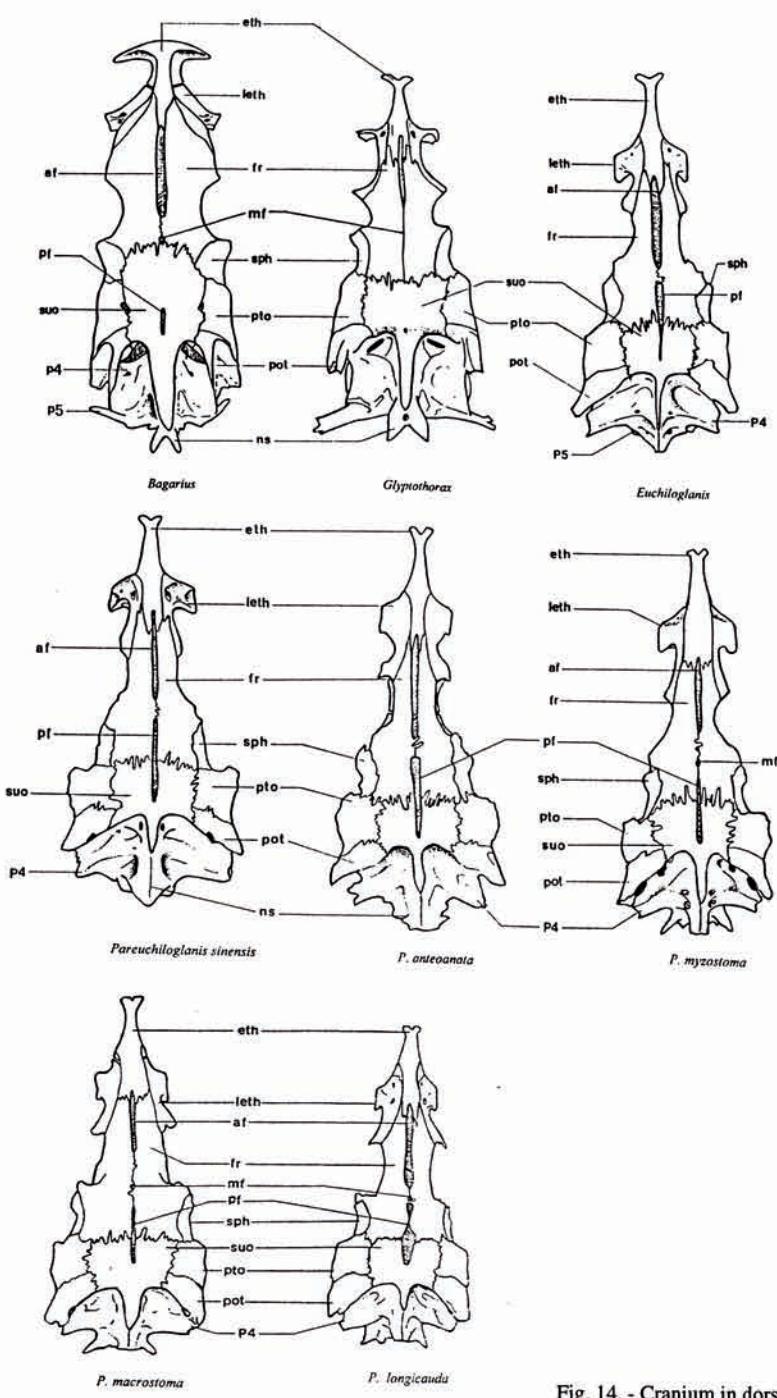


Fig. 14. - Cranium in dorsal view.

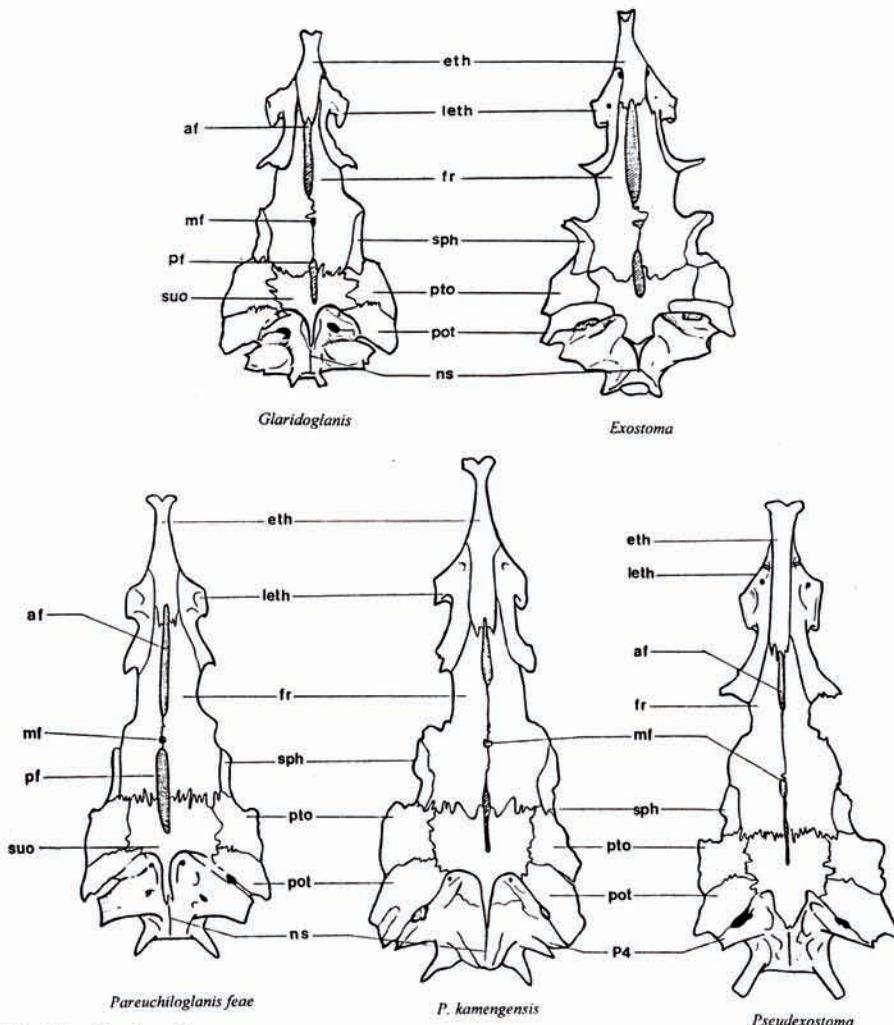


Fig. 14. - (Continued).

6. The posterolateral protrusion of the lateral ethmoid: in the out group this structure does not extend out the margin of the cranium (CS-0), but in the glyptosternoid fishes, in all the species, the posterior tip prolonged and extended out the margin to form a remarkable protrusion. This is the apomorphic condition (CS-1) (Fig. 14, leth).

7. The vomer: in *Bagarius*, the lateral margin of the head of the vomer forms the out margin of the anterior ventral side of the cranium (the head of the vomer is not limited by the ethmoid and the lateral ethmoid), but in all other studied species, the whole vomer is limited, enclosed by the lateral ethmoids and ethmoid; This is an apomorphy of *Bagarius* (CS-1).

8. The frontal: in *Diplomystes*, *Bagarius* and *Glyptothorax*, the width of the anterior and posterior parts is about equal (CS-0), but in all glyptosternoid fishes, the anterior part of the frontal is very narrow, the width is far smaller than that of the posterior part, this is the apomorphic condition (CS-1).

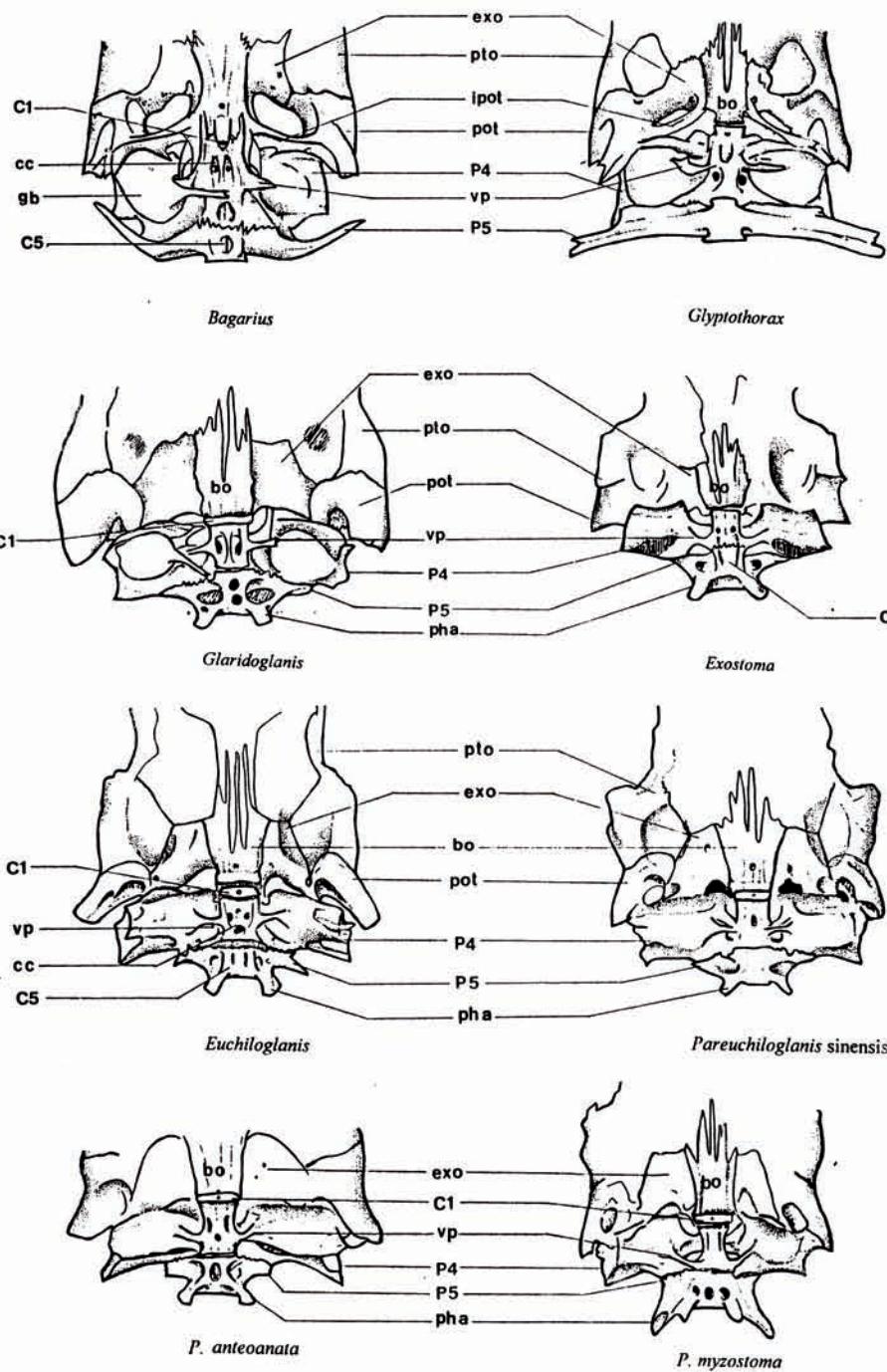


Fig. 15. - Posterior part of the cranium in ventral view.

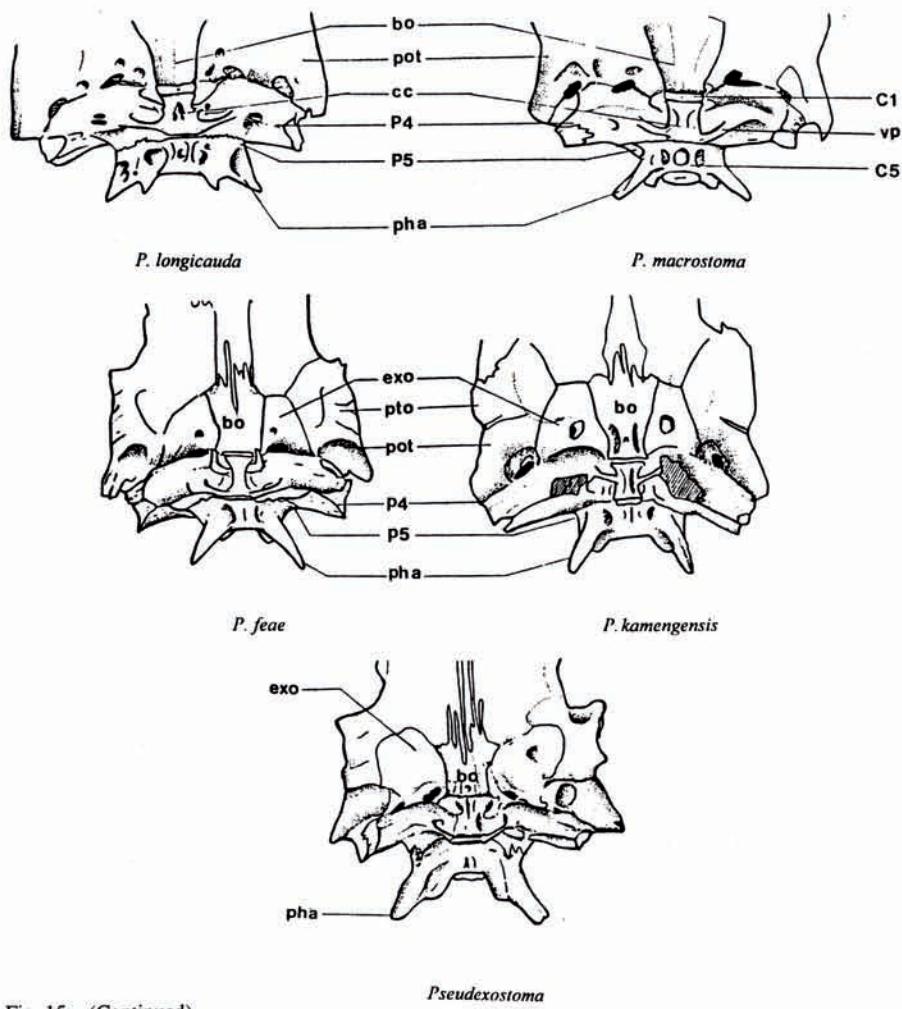


Fig. 15. - (Continued).

9. The ratio of the length and width of the sphenotic: in the out groups, the ratio is respectively about 1.5/1, 1.2/1 and 2/1 (*Diplomystes*, *Bagarius* and *Glyptothorax*), and in the glyptosternoid fishes this ratio is various, in some species the length being bigger: In *Glyptosternum*, *Euchiloglanis*, *Pareuchiloglanis sinensis*, *P. anteoanata* and *Pseudexostoma* it is 2/1; *P. feae* 2.8/1; in *Glaridoglanis*, *Exostoma*, *P. longicaudata* and *P. kamengensis* it is 3/1; in *P. myzostoma*, *P. macrostoma* it is 3 or 4/1. The increasing of the length is an apomorphy.

CS-0: this ratio is 1.2/1, 1.5/1, 2/1 and 2.2/1; CS-1: 2.8/1, 3/1 and 4/1 (Fig. 14, sph).

10. Contact of the sphenotic with the supraoccipital: in *Diplomystes*, *Bagarius* and *Glyptothorax*, the sphenotic directly gets contact to the supraoccipital by the suture (CS-0), whereas in all glyptosternoid fishes, except *Glyptosternum*, the sphenotic only connects to the frontal and pterotic; this is a synapomorphy of the glyptosternoid fish except *Glyptosternum* which retains the plesiomorphic condition (CS-1) (Fig. 14, sph).

11. The supraoccipital and the posterior fontanelle: in *Diplomystes*, the posterior fontanelle is marginated by frontal and suproccipital and its posterior end nearly extends to the posterior end on the supraoccipital, but in *Bagarius*, it is limited on the center of the supraoccipital, so as in *Glyptothorax*. In some species of this genus, the fontanelle is marginated only by supraoccipital (*G. fukianensis*, Yangtze river), but in the Indian species, *G. lonah*, it is marginated by frontal and the supraoccipital (Tilak, 1963b); the first condition is an apomorphy. In the glyptosternoid fishes, the fontanelle is marginated by frontal and supraoccipital, but the length of the fontanelle occupied in the supraoccipital is different: *Glyptosternum* 2/3, *Glaridoglanis* 2/3, *Exostoma* 1/3, *Euchiloglanis* 2/3, *Pareuchiloglanis sinensis* 2/3, *P. anteoanata* 2/3, *P. myzostoma* 2/3, *P. longicaudata* 1/2, *P. macrostoma* 1/3, *P. feae* 2/3, *P. kamengensis* 1/2, *Pseudexostoma* 1/3. The decreasing of the length of the supraoccipital is an apomorphy.

CS-0: the posterior fontanelle is marginated by frontal and suproccipital and its posterior end nearly extends to the posterior end on the supraoccipital; CS-1: same like in CS-0, but its length is only 2/3 of supraoccipital; CS-2: 1/2; CS-3: 1/3; CS-4: posterior fontanelle is limited on the center of the supraoccipital (Fig. 14, suo).

12. The posterior process of the supraoccipital: in *Diplomystes*, the posterior process has not a wide dorsal surface, unlike in *Bagarius*, where it forms a very wide surface, with $L/W=2.2/1$ and *Glyptothorax*, 3/1. In Glyptosternoid fishes, this ratio is various: *Glyptosternum*, thin, no surface as in the *Diplomystes*; in *Glaridoglanis*, short, taper; in *Exostoma*, wide and short, $L/W=1/1$; *Euchiloglanis*, taper, 5/1; *Pareuchiloglanis sinensis*, taper, 2.8/1; *P. anteoanata*, taper, 3/1; *P. myzostoma*, taper, 3/1; *P. longicauda*, widely taper, 2/1; *P. macrostoma*, widely taper, 2/1; *P. feae*, wide, 3.3/1; *P. kamengensis*, taper, 2/1, *Pseudexostoma*, taper, 1/1. According to the comparison with the out group, I consider that the evolutionary direction is from thin, without dorsal surface to the wide process surface.

CS-0: the posterior process has not a wide dorsal surface; CS-1: $L/W=5/1$; CS-2: 3.3/1, 3/1, 2.5/1, 2.8/1, 2.2/1, 2/1, CS-3: 1/1 (Fig. 14, suo).

13. The exoccipital: in *Diplomystes*, *Bagarius* and *Glyptothorax*, the exoccipital does not contact to the anterior margin of the 4th modified parapophysis directly (CS-0). In *Glyptosternum*, the exoccipital has a posterolateral process which attaches the anterior margin of the gasbladder capsule, the attaching area being very small, between the posterior margin of the cranium and the parapophysis, there is a wide space (CS-1). But in other glyptosternoid fishes, the attaching area is increasing and there is no large space between the skull and the parapophysis (CS-2). In *Pareuchiloglanis longicaudata* and *P. macrostoma*, the posterolateral process branched on each side, and with the inner one articulated to the 4th parapophysis, that represents the apomorphic condition (CS-3) (Fig. 15, exo).

14. The basioccipital: in *Bagarius*, on the ventral side of the posterior part of the basioccipital, the 1st vertebra and the complex centrum of the vertebra, the superficial plate-like bone is developed and covers these area; on the middle, an oval area is left. It makes the body of 1st, 2nd vertebrae can not be seen. This structure is only found in this genus (CS-1) (Fig. 15, bo).

15. The anterior and posterior fontanelle (af, pf); appear in *Glyptosternum*, *Euchiloglanis*, *E. davidi*, *Glaridoglanis*, *Pareuchiloglanis sinensis*, *P. robusta* and *P. sichuanensis*. In *Exostoma*, *Pseudexostoma* and the other species in the genus *Pareuchiloglanis*, except the 2 long fontanelles, between them, there is an aperture-like fontanelle (mf). It is obvious that the plesiomorphic condition (CS-0) is the possession of two

fontanelles and the apomorphic condition (CS-1) is the possession of three fontanelles (Fig. 14, af, mf, pf).

16. The lachrymal: in *Bagarius* and *Glyptothorax* the lachrymal is narrow and long, its length being about 1/3 of the maxilla; in *Glyptosternum*, it is thin and long, and attaches the autopatine with its posterior notched; in *Glaridoglanis*, it is long but a little wide, 1/3 of the maxilla; in *Euchiloglanis*, long and wide, 1/2.5 of the maxilla; in *Pareuchiloglanis sinensis*, it is wide, $L/W=1/2$; in *P. anteoanata*, it is wide; in *P. myzostoma*, it is short and wide, its length is 1/3 of the maxilla; in *P. longicaudata*, it is wide, and have 1/1.5 of the maxilla; in *P. macrostoma*, it is wide, and as long as the maxilla; in *P. feae*, it is wide and short, only 1/4 of the maxilla; in *P. kamengensis*, it is wide, $L/W=1.5/1$, also it is long, 1/1.7 of the maxilla. The increasing of the width and length is the evolutionary polarity. The specialized species support the soft tissue of the head by these enlarged bony plates.

CS-0: the lachrymal is narrow and long, 1/3 length of maxilla; CS-1: wide and long and CS-3: wide and not very long, $L/W=1/2$ (Fig. 16, lac).

17. Composition of the premaxilla: in *Bagarius*, the premaxilla is composed by two symmetric parts, each of them being composed by two bony plates, the inner one is equipped with a long ridge and the outer one is tapered posteriorly. All the bony plates are very compressed. In *Glyptosternum*, the structure is similar to that in *Bagarius*, but the two parts have longer attaching lines, the inner one having a protrusion whose free end is backward and tapered. The Glyptosternoid fishes have different conditions: in *Glyptosternum* and *Euchiloglanis*, the tooth band extend posteriorly, and each part of the premaxilla is composed by three or four bony plates individually; except these two genera, in all others, the premaxilla includes single bony plates on each half. This is the apomorphic condition.

CS-0: each premaxilla being composed by one bony plate; CS-1: two bony plates; CS-2: three plates and CS-3: four plates (Fig. 17, pmx).

18. The anterior process on dorsal side of the premaxilla: in *Diplomystes*, there is no protrusion or ridge on the dorsal face of the premaxilla whereas in *Bagarius*, there exists a transverse ridge, poorly developed on the dorsal face. In *Glyptothorax*, there is a short tapered protrusion with its free end transverse, undeveloped. But in most of the Glyptosternoid fishes, on each inner side of the premaxilla there is a developed protrusion with a forth free end which represents a derived character for this group. In different species, this protrusion varies: in *Glyptosternum*, *Pareuchiloglanis sinensis*, *P. anteoanata*, *P. myzostoma*, *P. longicauda*, and *P. macrostoma* the head of the protrusion is single; but in *Euchiloglanis*, *Pareuchiloglanis feae*, *P. kamengensis*, and *Pseudexostoma* the anterior process is double headed, the inner one being enlarged as a plate-like bone. In *Exostoma* and *Glaridoglanis*, this dorsal process is on the middle and undeveloped.

CS-0: no protrusion or ridge on the dorsal face of the premaxilla; CS-1: the head of the protrusion is single; CS-2: the anterior process is double headed; CS-3: this dorsal process is on the middle and undeveloped (Fig. 17, ap).

19. The shape of the tooth band on the premaxilla: in *Bagarius*, *Glyptosternum* and *Euchiloglanis*, this band is bent posteriorly, the stretching part is on the surplus bony plate (CS-0), but in *Glyptothorax*, this posteriorly stretching part is undeveloped (CS-1); in all other glyptosternoid fishes, the upper jaw tooth band is very limited, only on the single premaxilla (CS-2) (Fig. 17, pmx).

20. The maxilla: in *Diplomystes*, it is stout, bears the teeth and its inner end articulates the autopatine; in *Bagarius*, the maxilla is very thin and long, longer than the

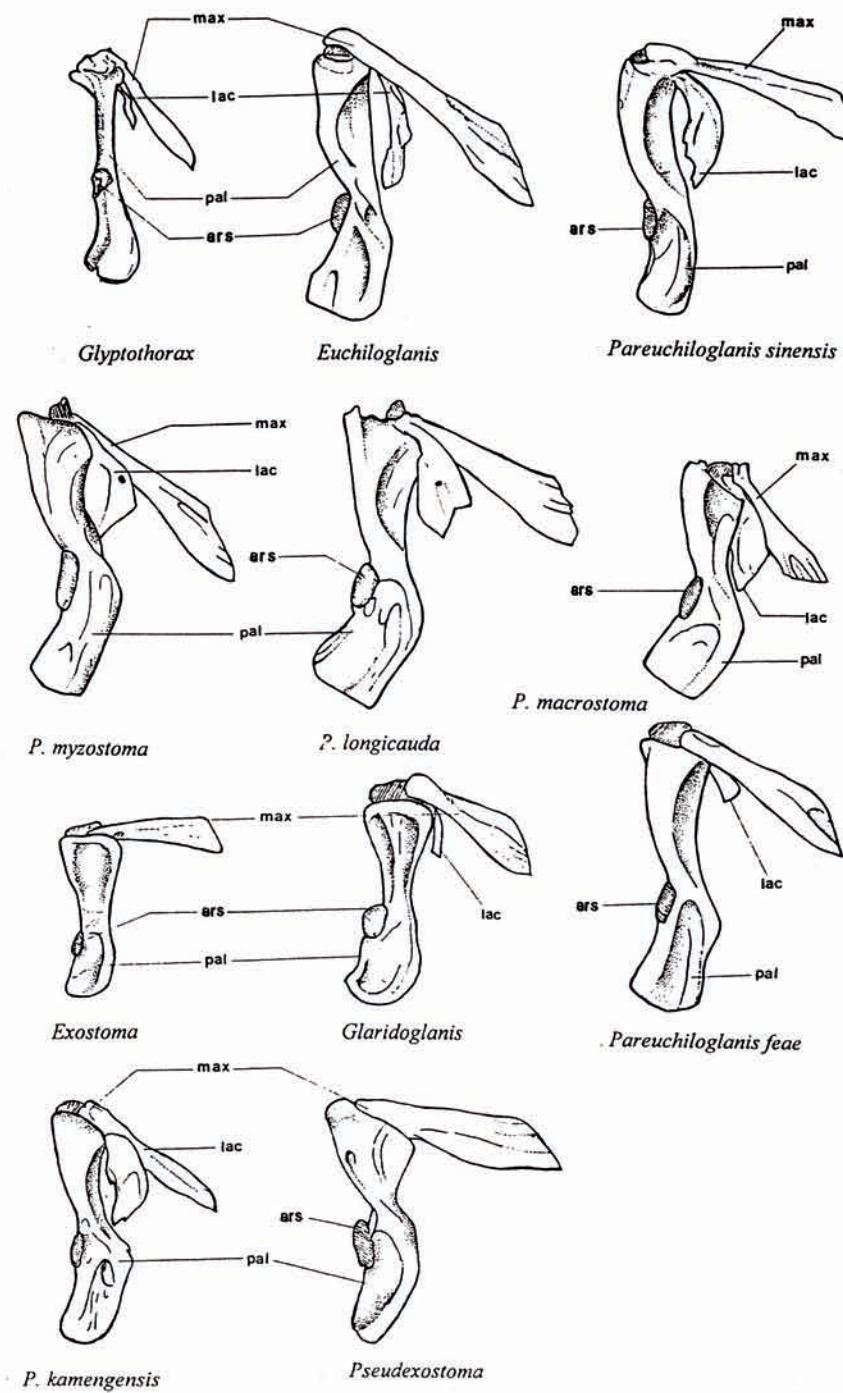


Fig. 16. - Palatine, maxilla and lachrymal.

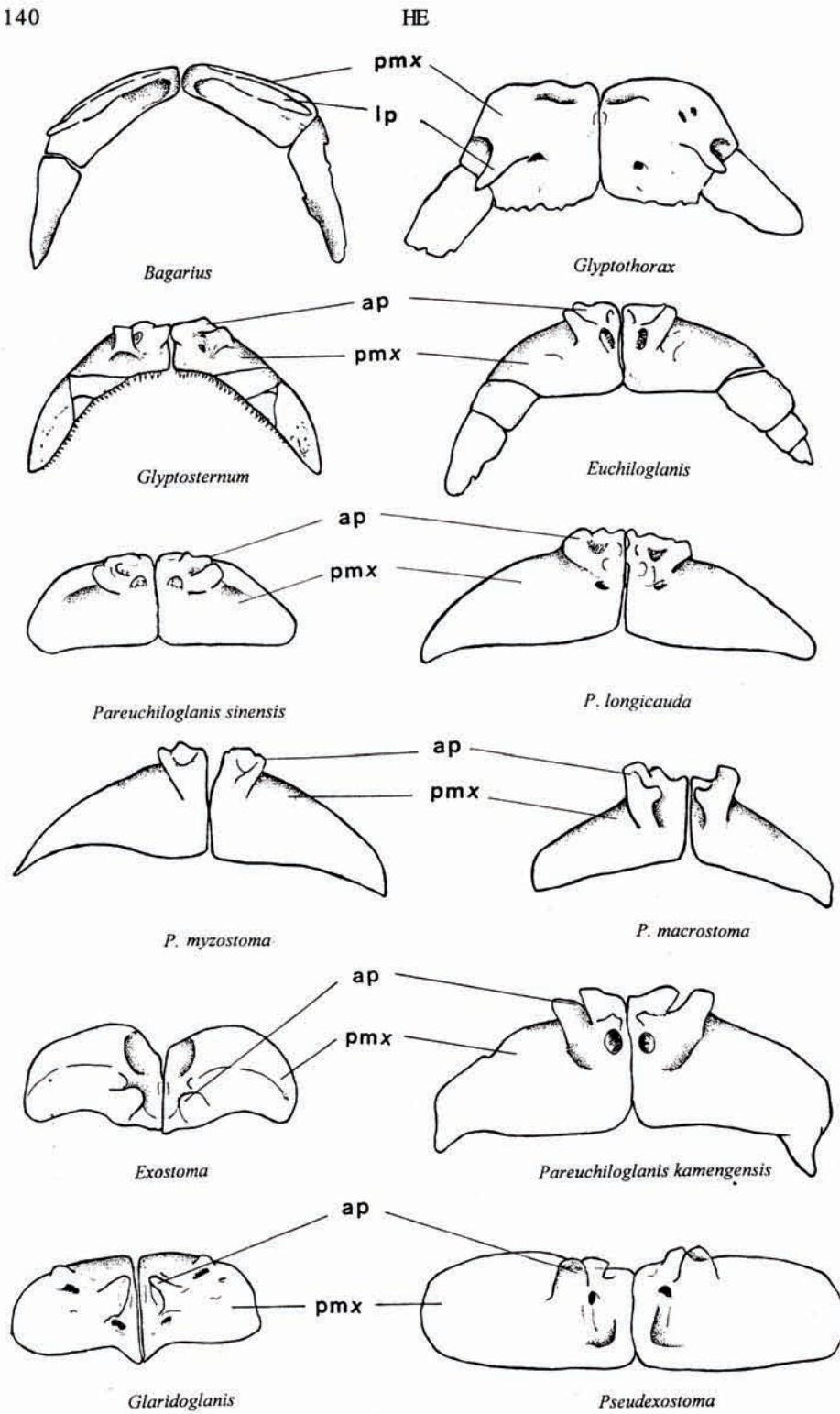
autopalatine; in *Glyptothorax*, the maxilla also is very thin but shorter than the autopalatine; in glyptosternoid fishes, the maxilla develops in different levels, posterior end is bifid or enlarged, etc. In *Glyptosternum*, the maxilla is very thin and long, $L/W = 6/1$ and the section of its anterior part is round but its posterior part is compressed; the other species have a maxillary enlarged posteriorly as fan-shaped, its width on the length being different: *Glaridoglanis*, 1/2; *Exostoma*, 1/3; *Euchiloglanis* 1/4; *P. sinensis*, 1/4.5; *P. anteoanata*, 1/3; *P. robusta* 1/2.2; *P. myzostoma* 1/3.8; *P. longicauda* 1/3; *P. macrostoma*, 1/3; *P. feae*, 1/4; *P. kamengensis*, 1/3; *Pseudexostoma*, 1/3. In the last 2 species, the posterior part of the maxilla is very strong and thick, but in other species it is very compressed. The evolutionary direction in the glyptosternoid is: from the long, thin bony bar to short, wide and then to the thick, short bony bar. This character corresponds to the changing of the maxillary barbel. In *Diplomystes*, this character is the apomorphic state.

CS-0: the maxilla is very thin and long, or $L/W=6/1$; CS-1: $L/W=1/4$, 1/4.5, 1/3.8; CS-2: $L/W=1/3$, 1/2.2 and 1/2 (Fig. 16, max).

21. The autopalatine: in *Bagarius* and *Glyptothorax* they are very similar each other: before the articulate facet for the lateral ethmoid, the autopalatine is round, thin and after this facet, it enlarges as a fan-like bony plate, its width being respectively 1/3, 1/2.5 length of the autopalatine (CS-0). In *Glyptosternum*, the first half of the autopalatine before the articulate also is round, with its head very strong and its width on the length is 1/2 with its posterior part fan-like shaped, its width on the length is also 1/2 (CS-1); the other glyptosternoid fishes have its first half autopalatine compressed, wide, and the posterior part fan-like, spoon-like (CS-2). In *P. feae*, *P. kamengensis* and *Pseudexostoma*, the autopalatine is stronger, the first half having a thick ridge on the inner side (CS-3). The specialized changing of stronger, enlarged and compressed is the apomorphic character (Fig. 16, pal).

22. The dentary: in *Bagarius* it is a very simple structure, from the head to the end, its width is nearly equal, thin and feeble, without a modified structure. In *Glyptothorax*, a similar condition can be found, but on the end of the dentary, just before the articular, there is an elevated ridge, weakly developed (CS-0); in glyptosternoid fishes, this structure is very developed and among the different species, there exist various conditions: in *Glyptosternum* and *Euchiloglanis*, the dentary is stronger than in the out group and on the posterior end of this bone the elevated ridge is thick and developed (CS-1). This is one of the apomorphic condition in glyptosternoid fishes. In *Exostoma* and *Glaridoglanis*, the anterior part of dentary is enlarged and thick, the elevated ridge is not very thick, but long and thin (CS-4). This character differs from that in *Glyptosternum*; this is another apomorphy; in the other Glyptosternoid fishes, except the elevated ridge, there exists another protrusion horizontally on the base of the elevated ridge; this protrusion is not very developed (CS-2) except in *Pseudexostoma*, *P. kamengensis*, and *P. longicauda* (CS-3). This evolutionary character indicated that these species and group are more specialized (Fig. 18, den).

23. The tooth band of the upper jaw: in *Glyptothorax* and *Bagarius*, the tooth band of the upper jaw stretches to each posterolateral side, but the stretched part is the segment, and on it the teeth also are born. This structure is called by Tilak (1963b) the 'posterior segment of premaxilla'. In the in-group, only *Glyptosternum* and *Euchiloglanis* have the stretched tooth band; this is a plesiomorphy (CS-0). The all other species own the narrow tooth band, also without any kind of posterior segment of premaxilla that may have disappeared in the evolutionary process; this is an apomorphy (CS-1).



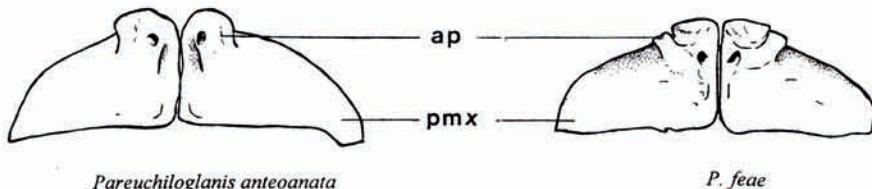


Fig. 17. - Premaxilla in dorsal view.

24. The ridge of the lower jaw: in the glyptosternoid fishes, there is a prominent ridge formed wholly by dentary. Most length of the lower jaw is formed by the dentary. In the out group, no ridge (*Bagarius*) or a small one (*Glyptothorax*) exists, the dentary only forming half length of the lower jaw, the second half being formed by the articular and the splenial. This is a synapomorphy (Fig. 18, den, art).

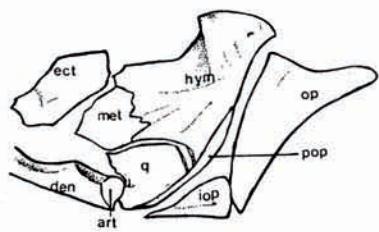
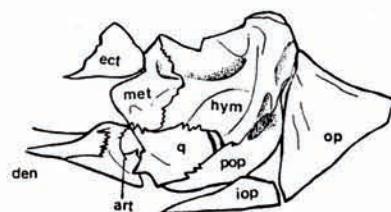
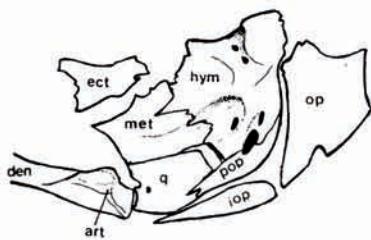
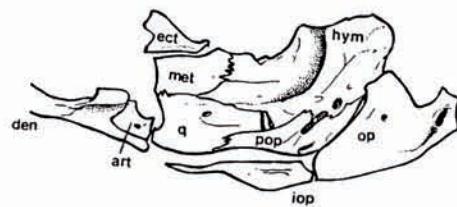
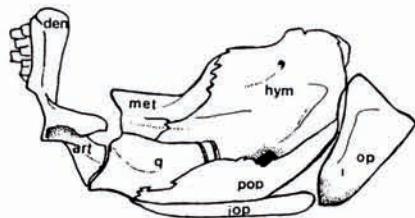
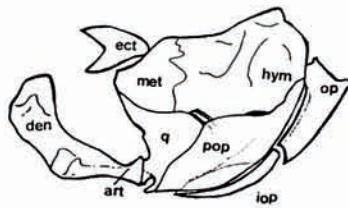
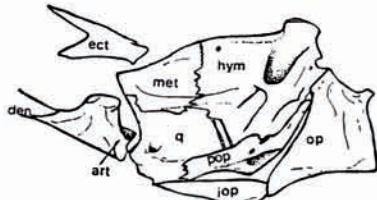
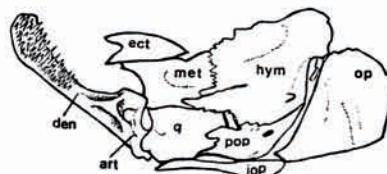
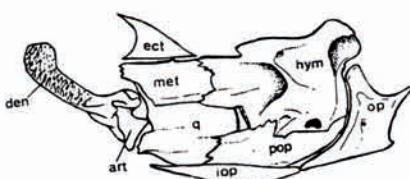
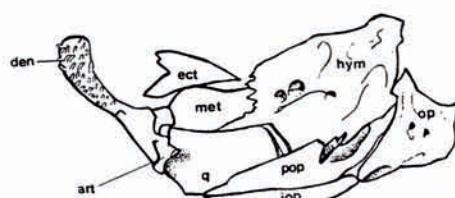
25. The teeth: in the out-group, the premaxillary and dentary teeth are conical, thin and long, without any kind of specialization. Even in most of the species and genera of the in-group, the teeth are also pointed, such as in *Glyptosternum*, *Euchiloglanis*, *Pareuchiloglanis*, and *Myersglanis*; this is a typical plesiomorphy (CS-0). But in *Glaridoglanis*, the teeth are very strong, just like the chisel, and their free end is blunt (CS-1). In *Exostoma*, the shape of the tooth is very complicate; its stem is very short, and its cap is a long plate with a ridge. This structure is called by Hora (1923) the oar-like teeth but, Chu (1979) named it the mixed tooth (CS-2). In *Pseudexostoma* and *Oreoglanis* they bear conical teeth and shovel-like teeth also. All these specialized teeth are stemmed from the pointed teeth, but their relationships are very difficult to decide. But *Pseudexostoma* and *Oreoglanis* bear the same type of tooth, so they share the synapomorphy (CS-3).

26. The articular: in the out-group, there is no any elevated ridge formed by the dentary; the length of the dentary is about equal to the length of the articular, or a little longer than that of the articular (CS-0). In most of the glyptosternoid fishes, there is a prominent ridge formed wholly by dentary, and the articular is very short and small, wedge-like, attaching to the posterior end of the dentary. This is an apomorphy (CS-1). But in *Exostoma* and *Glaridoglanis*, the dentary is not too much longer than the articular, and the elevated ridge is not very advanced; this is a plesiomorphic condition (CS-0) (Fig. 18, art).

27. The autopalatine: in the glyptosternoid fishes, the autopalatine is enormously developed, broad, strong and spatulated at both ends. It articulates with lateral ethmoid by its center and encloses posteriorly a cup shaped space (CS-1). But in the out-group, this autopalatine is not so strong; it is a long and thin rod articulating to lateral ethmoid by a point slightly posterior to its center (CS-0) (Fig. 16, pal).

28. The ectopterygoid: in the glyptosternoid fishes, it is smaller than the metapterygoid, and connected with the metapterygoid only by its thin posterior end (CS-1). On the contrary in the out-group, the metapterygoid is smaller (CS-0) (Fig. 18, ect, met).

29. The relationships of the ectopterygoid, metapterygoid and the hyomandibula: in the out-group, the posterior and the ventral margin of the ectopterygoid contact to the metapterygoid and hyomandibula with a fissure. Especially in *Bagarius*, the upper margin of the ectopterygoid is as high as the upper margin of the hyomandibula (CS-0). But in all the glyptosternoid fishes, except *Pareuchiloglanis kamengensis*, *P. gongshanensis* and *Pseudexostoma* (CS-0), the posterior tip of the ectopterygoid does not reach the hyomandibula; they are connected by a ligament. This is an apomorphic condition (CS-1) (Fig. 18, hym, ect, met).

*Glyptocephalus**Glyptosternum**Euchiloglanis**Pareuchiloglanis sinensis**Glaridoglanis**Exostoma**Pareuchiloglanis myosoma**P. longicauda**P. feae**P. kamengensis*

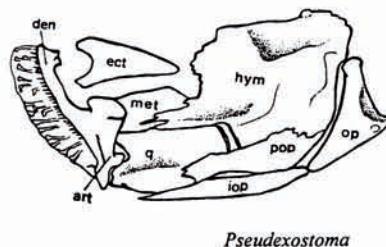


Fig. 18. - Suspensorium and lower jaw in lateral view.

30. The interoperculum: in all the glyptosternoid fishes, it is thin and long. It is as long as the length from the anterior tip of the dentary to its posterior end (CS-1). This character is very different from that in the out-group where the interoperculum is short, triangular and also a little broad (CS-0) (Fig. 18, iop).

31. The shape of the opercular: in glyptosternoid fishes, it is quadrilateral (CS-1), but in *Glyptothorax* and *Bagarius*, the opercular is triangular (CS-0). The former is apparently more specialized than the second (Fig. 18, op).

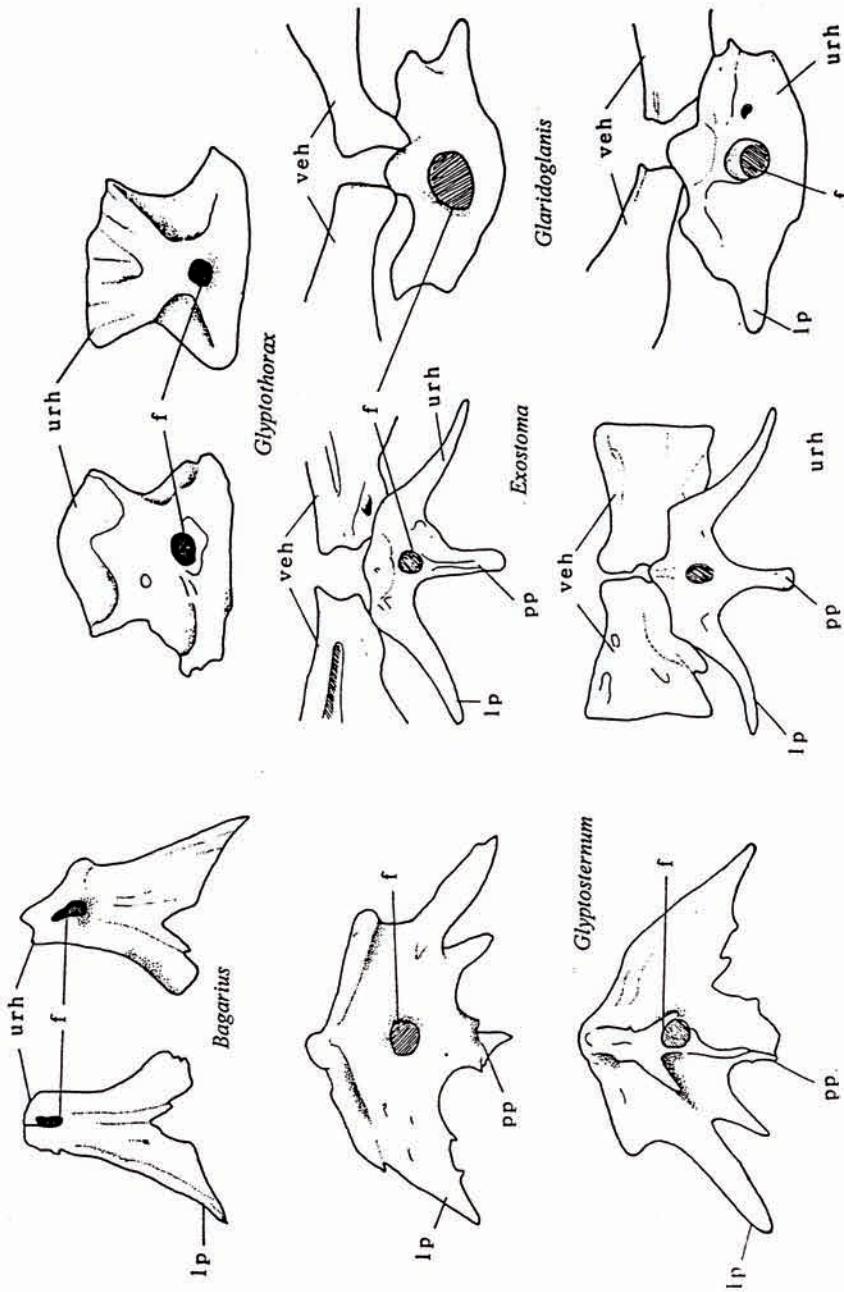
32. The ratio of length and width of the opercular: in *Glyptothorax* and *Bagarius*, the opercular is relatively bigger and has its length about equal to its width. *Glyptosternum*, *Euchiloglanis*, *Pareuchiloglanis sinensis*, *P. anteanalis*, *P. robusta*, *P. sichuenensis*, *P. macrotrema*, *P. longicauda* and *P. myzostoma* have the same opercular as in the out group; so it is the plesiomorphic condition (CS-0). In *Glaridoglanis*, *Exostoma*, *Pareuchiloglanis feae*, *P. kamengensis*, *P. gongshanensis* and *Pseudexostoma*, the opercular is relatively smaller, its width being far smaller than its length and its shape being sickle-like, represents the apomorphic character (CS-1) (Fig. 18, op).

33. The preopercular: in the out-group, the preopercular is very narrow and it is a long bony plate below the hyomandibular and the quadrate (CS-0). But in glyptosternoid fishes, this bony plate is very wide and its developing level is various: in *Euchiloglanis* and *Glyptosternum* it is comparatively narrow, undeveloped (CS-1), whereas in *Exostoma*, it is especially developed (CS-3). The other species range between these two conditions (CS-2) (Fig. 18, pop).

34. The hole between the preopercular and the hyomandibular: in glyptosternoid fishes, between the preopercular and the hyomandibular, there is a big hole (CS-1). In *Exostoma*, *Pseudexostoma* and *Glyptothorax*, this structure does not exist (CS-0). This is a plesiomorphy (Fig. 18).

35. The urohyal: in the out-group, there are only two posterior lateral protrusions (pp) on the urohyal. In *Bagarius* this structure is more developed than in *Glyptothorax* (CS-0). In *Glyptosternum* and *Exostoma* the urohyal is tri-branched (CS-1). The urohyal of *Glaridoglanis* has not the posterior protrusions but only two postero-lateral processes (CS-2). In *Euchiloglanis*, *Pareuchiloglanis*, and *Pseudexostoma*, the postero-lateral processes are lacking and only the posterior process (pp) is developed (CS-3). The anatomy of the in-group is the apomorphic character and the tribranch is more primitive (Fig. 19, urh).

36. The numbers of the branchiostegal rays: in *Bagarius bagarius* it is 12-13, they are very thin and long and their proximal end attaches the ceratohyal and the epihyal. In *Glyptothorax*, these rays are 8. In the glyptosternoid fishes, *Glyptosternum* has 7 rays, *Glaridoglanis* and *Exostoma* have 8 rays (CS-0), whereas in *Euchiloglanis*,



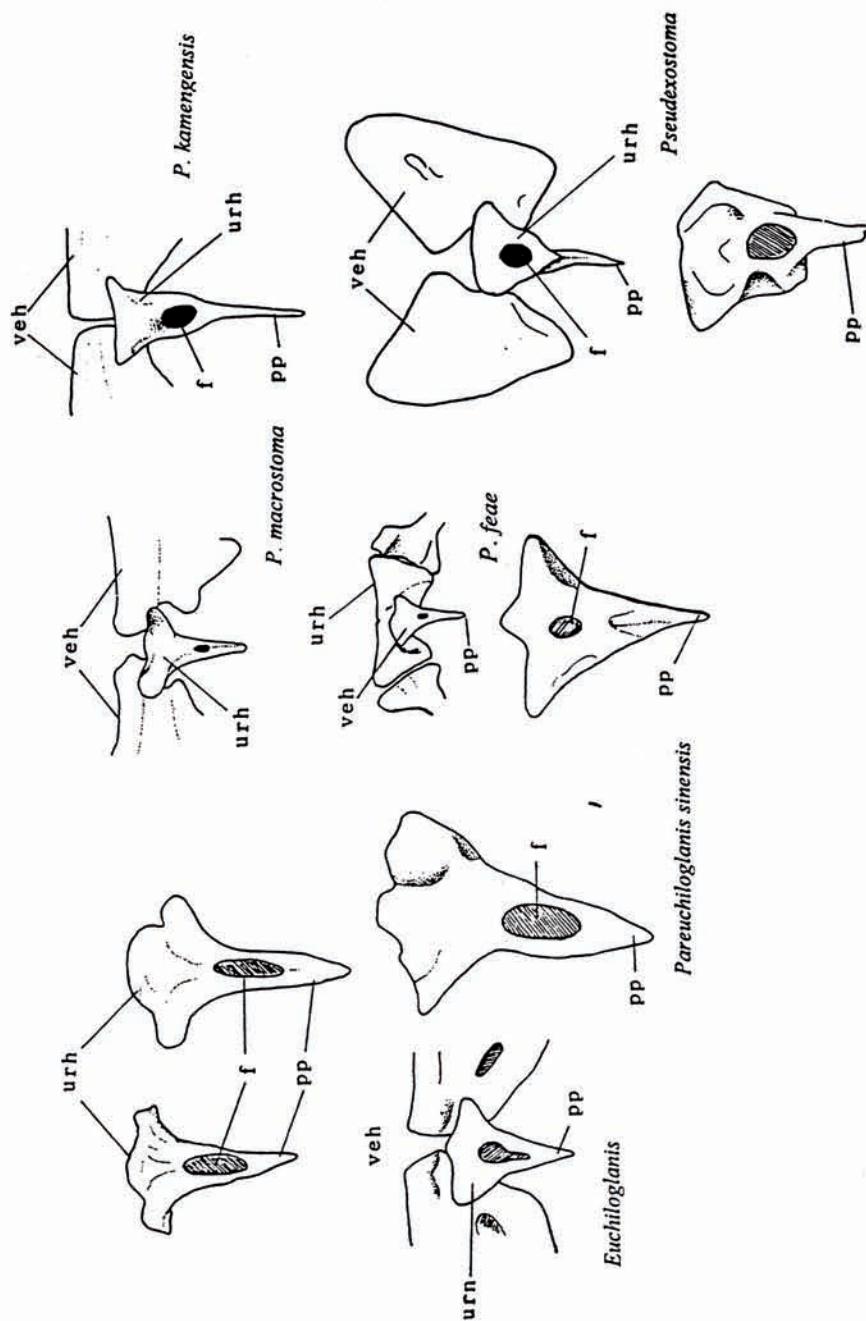


Fig. 19. - Urohyal.

Pareuchiloglanis sinensis, *P. anteanalis*, *P. robusta*, *P. macrostrema*, *P. longicauda* and *P. myostoma* there are 6 rays (CS-1); but in *P. feae*, *P. kamengensis*, *P. gongshanensis*, and *Pseudexostoma*, there are only 5 rays (CS-2). Based on the out-group comparison, the reduced number of the branchiostegal rays is an advanced character.

37. The dorsal neural spine of the 4th vertebra: in the glyptosternoid fishes, it is undeveloped, plate-like, single, and is not connected to the proximal radial of the dorsal fin; there is not distinction between the 4th neural spinal and the bony ridge of the skull (CS-1). But in *Glyptothorax* and *Bagarius*, even in all other sisoroid fishes, this dorsal neural spine is very developed, bifid, and gets contact with the proximal radials of the dorsal fin. The bony ridge connecting the compound vertebra and the 4th neural spine is high and separated completely (CS-0). Apparently, the glyptosternoid degrades its powerful dorsal neural spinal of the 4th vertebra due to the bottom dwelling (Fig. 14, ns).

38. The opening of the capsule for the gasbladder: in most of the glyptosternoid species, except *Glyptosternum*, the 4th parapophysis forms a bony cylinder opened laterally. This is an apomorphic condition (CS-1). Apparently, in *Glyptosternum*, the bony cylinder is not closed on its posterior side, as in the out-group, the partial capsule opening both ventrally and laterally (CS-0) (Fig. 15, P4).

39. The ventral opening of the gasbladder capsule: in the out-group, the bony capsule, formed by the parapophysis of the 4th vertebra, is not complete and it only encloses the dorsal and anterior face of the gasbladder. On its posteroventral face, the capsule is opened. In the genera *Glyptosternum*, *Glaridoglanis*, and *Exostoma* this structure is similar (CS-0), but in the genera *Pareuchiloglanis*, *Euchiloglanis*, *Pseudexostoma*, and *Oreoglanis*, the bony capsule is all closed except the two lateral openings; possession of the complete capsule is obviously an apomorphy (CS-1) (Fig. 15, P4).

40. The posterior opening of the gasbladder capsule: in the species *Pareuchiloglanis feae*, *P. kamengensis*, and *P. gongshanensis*, there exists an opening on the posterior face of the capsule, and through this opening, the white gasbladder tissue can be seen. This opening is not found in any other species and I treat it as a synapomorphy of these species (CS-1) (Fig. 15, P4).

41. The articulated-like protrusion on the anterior margin of the bony capsule for the gasbladder: in *Pareuchiloglanis macrostoma* and *P. longicauda*, there is a protrusion on the anterior margin of the capsule, for articulation with the posterior margin of the exoccipital. This articulation can also be seen in *Pseudexostoma* and I consider it as an apomorphy (CS-1) (Fig. 15, P4).

42. The relationship between the bony capsule for the gasbladder and the posttemporal: in the out-group, the capsule gets contact with the exoccipital only with its inner side of the anterior margin and the fossa between them is very clear; but the outer side of the anterior margin of the capsule is not connected to the posttemporal. So, between the posterior margin of the skull and the anterior margin of the capsule, on each side, there is an open groove, to which the cleithrum connects with the skull. This organization can be found in *Glyptosternum*, *Euchiloglanis*, *Glaridoglanis*, *Exostoma*, *Pareuchiloglanis anteanalis*, *P. robusta*, *P. sichuanensis* and *P. kamengensis*, and it represents the plesiomorphic condition (CS-0). In *Pareuchiloglanis sinensis*, *P. macrostrema*, *P. longicauda*, *P. myostoma*, *P. feae*, *P. gongshanensis* and *Pseudexostoma*, the outer side of the anterior margin fused to the posttemporal. As a result, between the skull and the capsule on each side, there is a hole to accept the cleithrum. This is the apomorphic condition (CS-1) (Fig. 15, pot, P4).

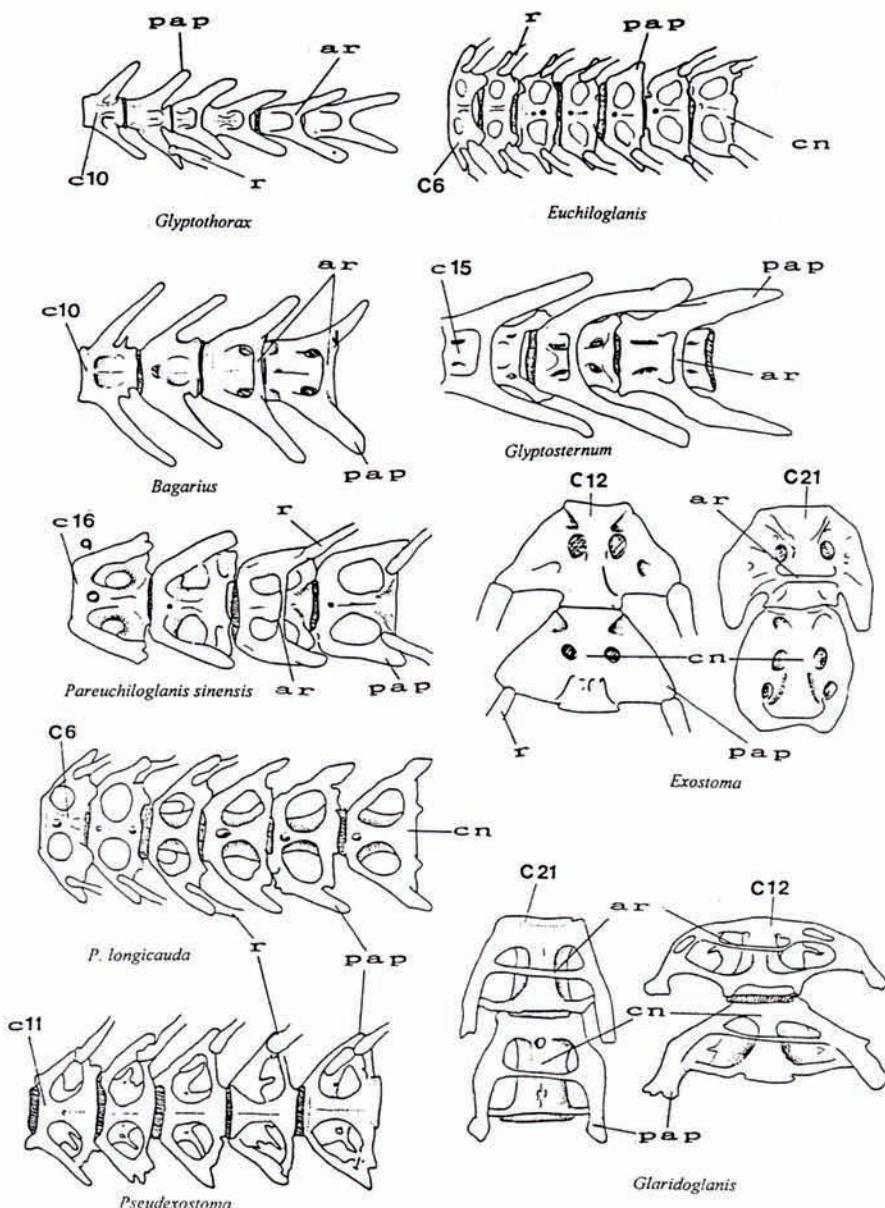
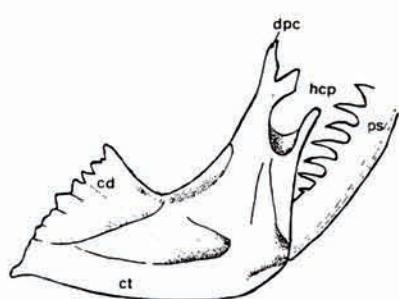
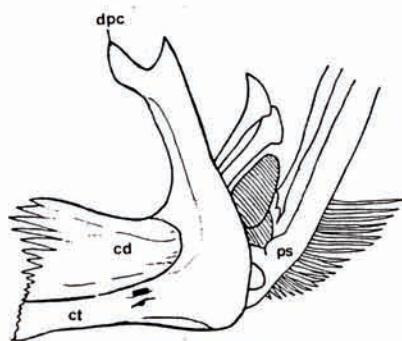
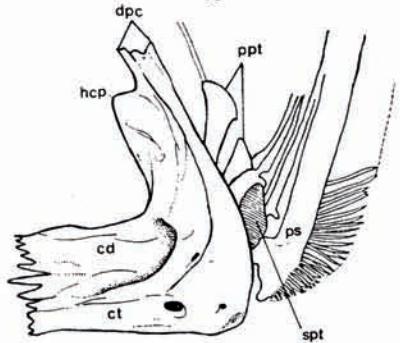
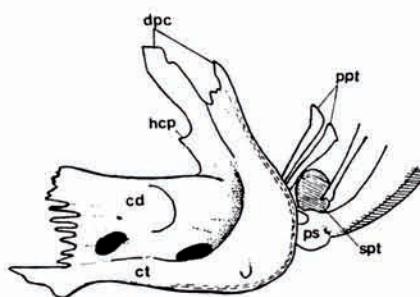
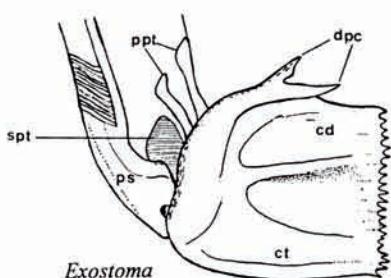
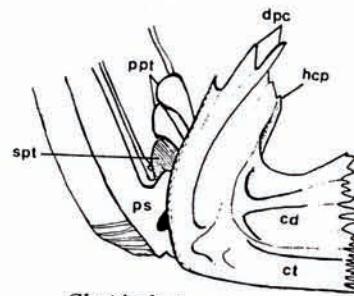
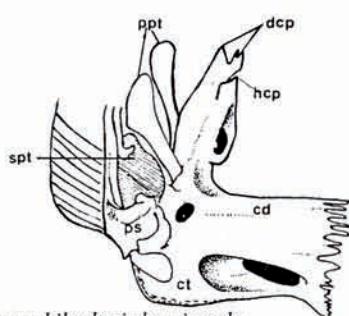
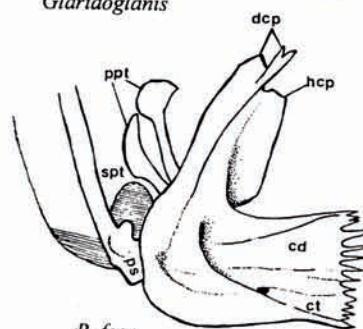


Fig. 20. - Vertebræ in ventral view.

43. The arch: in *Glyptothorax*, *Bagarius*, *Glyptosternum*, *Glaridoglanis*, *Exostoma*, *Pareuchioglanis sinensis*, and *P. anteanalis* on the ventral side of the abdominal vertebra centrum, there is an arch (ar) whereas in the other species and genera of glyptosternoid fishes, such a structure is lacking. I treat this absence as an apomorphy (CS-0).

*Glyptothorax**Euchiloglanis**Pareuchiloglanis sinensis**P. myzostoma**Exostoma**Glaridoglanis**Pareuchiloglanis longicauda**P. feae*

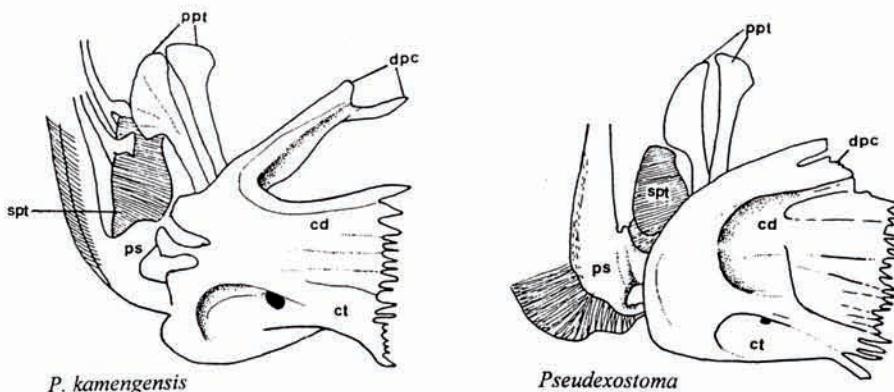


Fig. 21. - Pectoral fin skeleton.

The arch in *Pareuchiloglanis sinensis*, *P. anteanalis*, *Glaridoglanis*, and *Exostoma* is very thin, especially in *Exostoma*, *Pareuchiloglanis sinensis* and *P. anteanalis*, this structure only exists on the last abdominal vertebra (CS-1) (Fig. 20, ar).

44. The post-haemapophysis of the 5th vertebra: in the out-group, the post-haemapophysis of the 5th vertebra are undeveloped (CS-0); in *Glyptosternum*, *Glaridoglanis*, *Exostoma*, *Pareuchiloglanis sinensis*, *P. anteanalis*, *P. robusta*, and *P. sichuanensis*, there are a pair of short post-haemapophysis; this character is treated as the apomorphy (CS-1). In the other species of the genera *Pareuchiloglanis* and *Pseudexostoma*, the post-haemapophysis are very developed, far exceed the post margin of the vertebra. I consider this a more advanced apomorphic condition than in the precedent species (CS-2) (Fig. 15, pha).

45. The 5th parapophysis: in glyptosternoid fishes, it is undeveloped and far shorter than the 4th parapophysis (CS-1), but in *Bagarius* and *Glyptothorax*, it is very developed, longer than the 4th parapophysis (CS-0). Compared to Diplomystidae, it is apparent that the glyptosternoid is an apomorphic one (Fig. 15, P5).

46. The inferior limb of the posttemporal: in the out-group, even in all other sisoroid fishes, the posttemporal bears an infer-lateral limb which is thin and long and its inner end attaches the base of the basioccipital (CS-0). But in glyptosternoid fishes, the posttemporal is an unbranched bony plate, without the inferior limb, the anterior margin of the gasbladder capsule contacting to the exoccipital. This is a synapomorphy of the glyptosternoid fishes (CS-1) (Figs 14, 15, pot).

47. The pectoral spine: in the out-group, it is a hard spine with its posterior margin equipped with serration (CS-0); but in the glyptosternoid, it gives off many pointed protrusion which is unmineralized bony structure along the anterior margin which are enveloped in the skin of the fin. This character made it easily to identify the glyptosternoids from other sisoroid fishes (CS-1).

48. The number of the branched pectoral fin rays: in *Bagarius*, this number is 11, 6-12 in *Glyptothorax*, 10-11 in *Glyptosternum*, *Glaridoglanis* and *Exostoma*, 12-14 in *Euchiloglanis*. In *Pareuchiloglanis*, it is 13-16; with 14-16 in *P. feae*, *P. kamengensis*, *P. gonshanensis* and 13-15 in the others. In *Pseudexostoma* and *Oreoglanis*, there are 16-18 branched pectoral fin rays. According to the out-group comparison, the increasing number of the pectoral fin rays is an advanced character.

CS-0: 11, 6-12, 10-11 and 12-14; CS-1: 13-16, 14-16, 13-15; CS-2: 16-18.

49. The pectoral girdle: in *Glyptothorax* and *Bagarius*, the posterior dorsal margin of the pectoral girdle forms an obtuse angle with its anterior margin. The antero-medial part formed by the cleithrum and the coracoid is not very wide (CS-0); but in the glyptosternoid fishes, this angle is acute, and the antero-medial is very wide (Fig. 21). Referring to *Bagrus bayad* (Mo, 1991), the character status of the glyptosternoid is advanced (CS-1).

50. The cleithrum: in *Exostoma* and *Pseudexostoma*, it is enlarged so much that there is no free posterior dorsal process. This is a specialized character (CS-1), but according to other character comparison, this character may be developed independently in these two species (Fig. 21).

51. The humero-cubital process of the pectoral girdle: at about the middle region of the posterior border of the cleithrum, the humero-cubital process is given off. In *Bagarius* and *Glyptothorax*, this process is on the outside of the postero-dorsal process, not very developed. Its base is narrow and its free end is pointed (CS-0). In most of the glyptosternoid, this process is on the inner side of the posterodorsal process, and is a wide, thin bony plate; its free end is not pointed. But in *Exostoma* and *Pseudexostoma*, the base of the humero-cubital process is very wide, its posterior margin nearly approaches the posterior end of the cleithrum and there is no free end. Apparently, most of the glyptosternoid possess the apomorphic character (CS-1), and *Exostoma* and *Pseudexostoma* have a much more specialized condition (CS-2) (Fig. 21, hcp).

52. The 1st proximal of the dorsal fin: in *Bagarius* and *Glyptothorax*, the upper end is Y-shaped, flat bony plate, it is horizontal; the posterior margin of this Y-shaped bone attaches tightly to the anterior margin of the 2nd proximal. In *Glyptosternum* and *Pareuchiloglanis sinensis*, this upper horizontal part is reduced and only a feeble posterior limb attaches the 2nd proximal (CS-0); in other glyptosternoid fishes, this upper horizontal end is reduced completely (CS-1); the first two species of glyptosternoid fishes in this character are primitive, own the plesiomorphy (Fig. 22, pr1).

53. The 2nd proximal of the dorsal fin: in *Bagarius* and *Glyptothorax*, it has a wide lateral process; in *Glyptosternum* and *Euchiloglanis*, this process is a little reduced (CS-0) and in all other glyptosternoid fishes, it is very much undeveloped, and its shape is tapered, not wide (CS-1) (Fig. 22, pr2).

54. The 1st dorsal spine of the dorsal fin: in *Bagarius* and *Glyptothorax*, the 1st dorsal spine is a free V-shaped bone (CS-0) whereas in most of glyptosternoid fishes, there is no free 1st dorsal spine. It is modified as a thin rod and emerged with the posterior process of the 1st proximal of the dorsal fin and the anterior process of the 2nd proximal of the dorsal fin and also crosses the hole on the base of the 2nd dorsal spine. This structure can lock the 2nd dorsal spine. This is the apomorphic condition (CS-1). But in *Glyptosternum* and *Exostoma*, I can not find this rod-like 1st dorsal spine (CS-2) (Fig. 22, dsp1).

55. The 2nd dorsal spine of the dorsal fin: in *Bagarius*, on the anterior margin of the 2nd dorsal spine, there are some weak serrations, but in *Glyptothorax*, the anterior margin is glossy (CS-0); in glyptosternoid fishes, on the anterior margin, it gives off many feather-like soft cartilaginous rays (CS-1). This character is similar to the character 47 on the pectoral fin, and, of course, is an apomorphy (Fig. 22, dsp2).

56. The caudal skeleton (Fig. 23): in *Diplomystes*, there are six separate hypurals (HU1-6) (CS-0), but in *Glyptothorax* and *Bagarius*, most of them are fused; the fused pattern is PH; HU1+HU2; HU3+HU4; HU5 (CS-1). In *Glyptosternum*, the parhypural also fused with the hypurals and the fused pattern is: PH+HU1+HU2, HU3+HU4, HU5

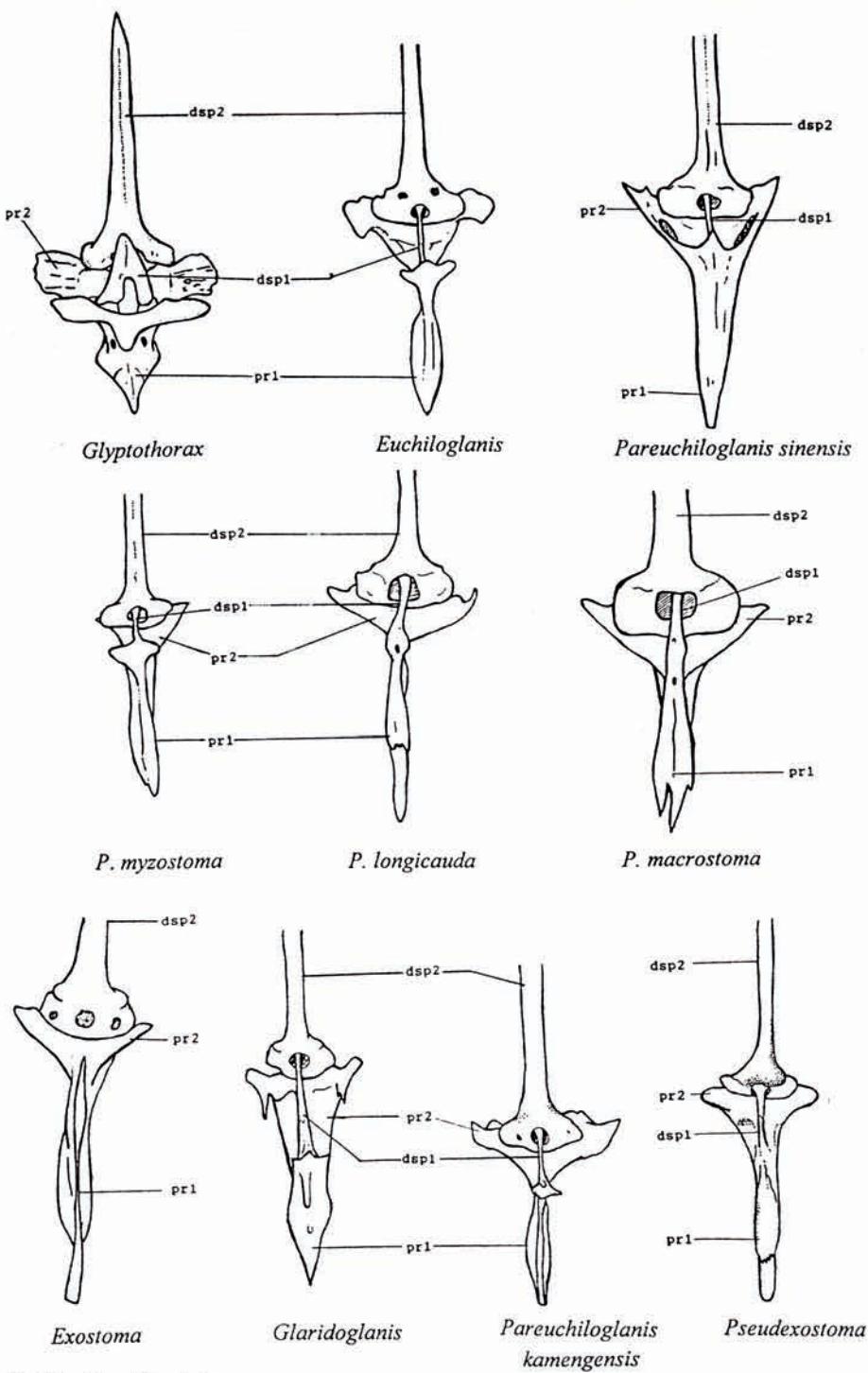


Fig. 22. - Dorsal fin skeleton.

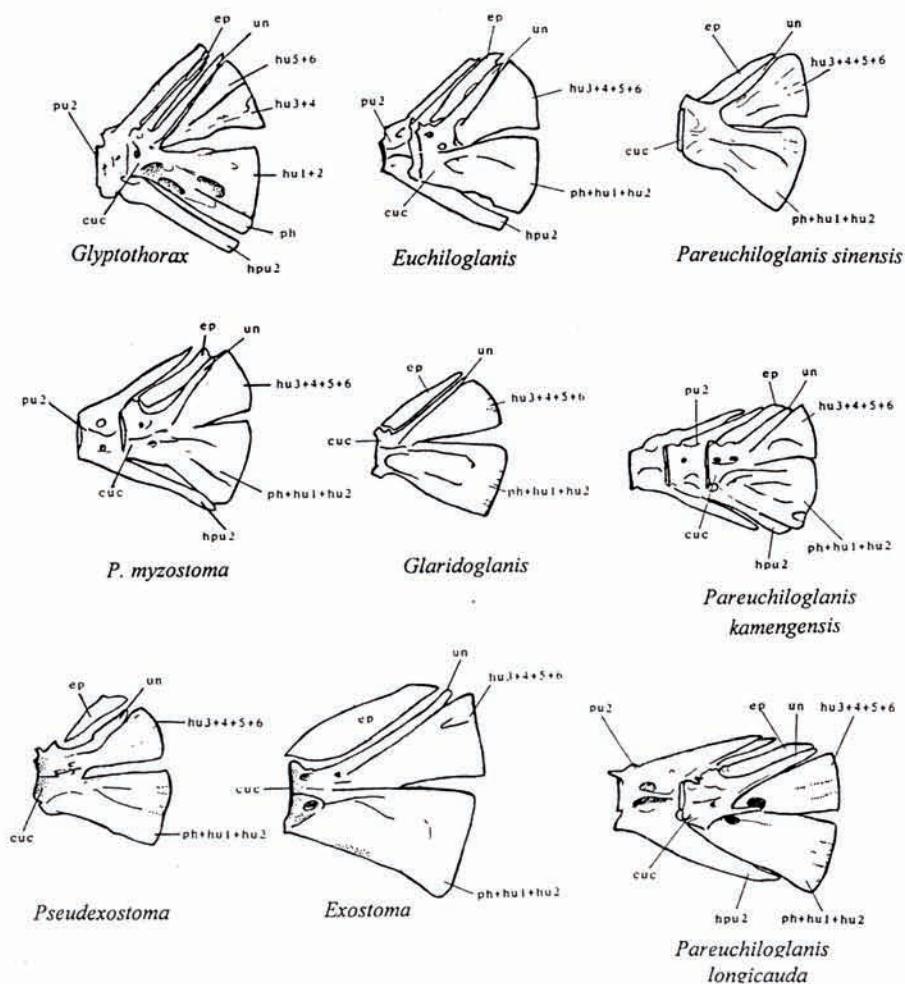


Fig. 23. - Caudal fin skeleton in lateral view.

(HU5+HU6?). In all other glyptosternoid fishes, the fused pattern is PH+HU1+HU2; HU3+HU4+HU5+HU6? (CS-3). In *Glyptosternum* only, there is a free hypural (Fig. 9); this is the plesiomorphic condition (CS-2), and it also indicates that *Glyptosternum* is a primitive genus.

57. The gill opening: in *Bagarius*, *Glyptothorax* and *Glyptosternum*, the gill opening extends to the ventral surface of the fish (CS-0); Chu (1979) classified the gill openings of the glyptosternoid fishes into three types: the big type, middle and small types. The gill opening of *Euchiloglanis*, *Glaridoglanis*, *Pareuchiloglanis longicauda*, *P. macrostrema* and *P. poilanei* is middle type, its lower angle reaching the lower part of the base of the pectoral fin (CS-1); in the other species belonging to *Pareuchiloglanis*, *Pseudexostoma* and *Exostoma*, the gill opening is very small, its lower angle only

reaches the middle point of the base of the pectoral fin (CS-2); the evolutionary polarity is reduction of the gill opening from big to small under the stress of the environment.

58. The mouth sucker: most of the species in the out-group and in-group do not have the mouth sucker, and the labial fold is continuous. This is a plesiomorphic state (CS-0). But in *Exostoma*, *Pseudexostoma*, *Myersglanis* and *Oreoglanis*, the lips specialized as a sucker, and the labial fold continuous, represent an apomorphy (CS-2); in *Pareuchiloglanis feae*, *P. kamengensis*, and *P. gongshanensis*, the lateral leaf of the lower lip is developed, and there is a groove between the lateral leaf and the base membrane; so the lateral leaf is semi-free. Actually this is a kind of primitive mouth sucker (CS-1). It is an advanced character, but it is not as specialized as in *Exostoma*.

59. The maxillary barbels: in the out-group, the barbels on the mouth angle are very long and thin, also their base is very narrow, such as in *Glyptothorax* and *Bagarius*. In the in-group, the barbels on the mouth angle of *Glyptosternum*, *Euchiloglanis*, *Glaridoglanis*, *Exostoma* and *Myersglanis* are similar to that in the out-group, but their base becomes a little wide and their end is thin and long (CS-0). In *Pareuchiloglanis*, most of the species also have this kind of thin and long barbels (CS-1), but the barbels of *P. kamengensis* and *P. gongshanensis* are round plate with a very short tip; their length is equal to their width (CS-2), and in *Pseudexostoma* and *Oreoglanis*, the barbels are round plate and there is no tip (CS-3). I can find that the thin and long barbels exist in out- and in-group. It is a plesiomorphic character whereas the round plate-like barbel is apomorphic.

60. The distance of the pectoral fin and the ventral fin: in the out-group and most of the in-group, the end tip of the pectoral fin does not reach the origin of the ventral fin (CS-0); but in *Pareuchiloglanis kamengensis*, *P. gongshanensis*, *Pseudexostoma* and *Oreoglanis*, the end of the pectoral fin overlaps the ventral fin (CS-1). This is interpreted as an apomorphy.

THE MATRIX AND THE CLADOGRAM

Table I is a data matrix compiled from the characters described in the previous section. Figure 24 is the cladogram produced from processing the data matrix on the Hennig 86 computer program. Based on this cladogram the following relationships are hypothesized:

(1) Glyptosternoid fishes form a monophyletic group defined by 13 synapomorphies (characters 6, 8, 23, 26, 27, 29, 30, 37, 43, 44, 45, 47 and 53).

(2) *Glyptosternum* is interpreted as the most primitive genus. All the other sisoroid fishes are suggested to have descended from it. This result corresponds to that of Hora (1952) and Chu (1979).

(3) Some external characters are adaptive characters, so they are based on the ecological reason, resulting an incongruence with the evolutionary polarity stemmed from the osteology: such as the posterior labial fold, mouth sucker, but these have been treated as systematic characters and used to produced an evolutionary tree (Chu, 1979).

(4) Some of the characters (character 58) occur in a group of taxa including *Exostoma*, *Glaridoglanis*, *Pseudexostoma*, and *Oreoglanis* which appear to have gained a number of derived features by convergence. My character analysis indicated that some specialized characters (such as the mouth sucker, continuous labial fold) of the *Exostoma* and *Glaridoglanis* are derived directly from the primitive status. They have not systematic relationships with the *Pseudexostoma* and *Oreoglanis*.

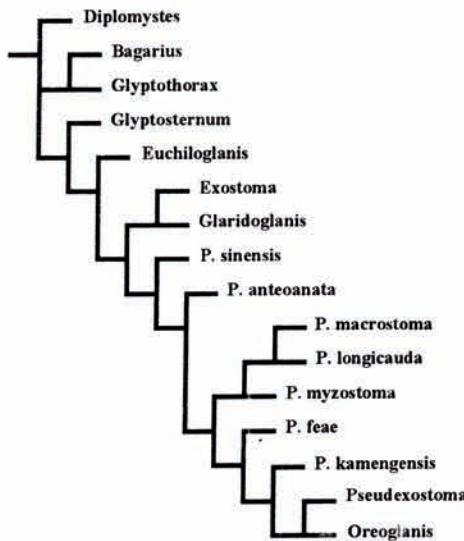


Fig. 24. - Cladogram of the glyptosternoid fishes.

(5) The genus *Pareuchiloglanis* is not a monophyletic group in the cladogram. The monophyly is only formed when *Pseudexostoma* and *Oreoglanis* are added.

Table I. - Data matrix of the glyptosternoid fishes for Hennig 86.

	0000000001 1234567890	111111112 1234567890	222222223 1234567890	333333334 1234567890	444444445 1234567890	555555556 1234567890
<i>Diplomystes</i>	0000000000	00000?0000	0?0000000	0000?0000	00????00?0	?000000000
<i>Bagarius</i>	0300001000	4201001001	0000000000	0000000000	0000000000	0000010000
<i>Glyptothorax</i>	2010000000	4300001511	0000000000	0000000000	0000000000	0000010000
<i>Glyptosternum</i>	2211010100	1010003101	1101011111	1010100000	0011110101	1002120000
<i>Glaridoglanis</i>	1111101011	1420010125	2411101111	1120201100	0011110101	1111131100
<i>Exostoma</i>	1111010111	3420120424	2411201111	1131101100	0011110111	2112132200
<i>Euchiloglanis</i>	1013010101	1020012323	2101011111	1010311110	0011111010	1101131000
<i>Pareuchiloglanis sinensis</i>	1021010101	1220020422	2211011111	1020311110	0111111110	1011132010
<i>P. anteoanata</i>	2013110101	1220020424	2211011111	1020311110	0011111110	1111132010
<i>P. myzostoma</i>	0022010111	1220120323	2211011111	1020311110	0112111110	1111132010
<i>P. longicauda</i>	1011110111	2330120124	2311011111	1020311110	1112111110	1111131010
<i>P. macrostoma</i>	1012110111	3330120224	2211011111	1020311110	1112111110	1111131010
<i>P. feae</i>	1012110111	1220120423	3211011111	1120321111	0112111210	1111132110
<i>P. kamengensis</i>	0022110111	2320120424	3311011101	1120321111	0012111210	1111132121
<i>Pseudexostoma</i>	0112110101	3420120424	3311311101	1121321111	1112111211	2111132231
<i>Oreoglanis</i>	0112110101	3420120424	3311311101	1121321111	1112111211	2111132231

CONCLUSION AND DISCUSSION

It was considered that the most primitive genus of the family Sisoridae is *Bagarius*. Hora (1939) wrote: "the palaeontological records from South-Eastern Asia show that *Bagarius bagarius* has persisted through a period of 5 million years with no great change in its appearance and has been called a "living fossil". Actually, it is the only known genus which has the fossil record, the time is in the Pliocene, its primitive position in this family is indisputable at present time". In 1952, Hora wrote: "the group of Glyptosternoid fishes originate from *Glyptothorax*-like ancestors under the stress of strong currents and necessity for more efficient mechanism of adhesion". Chu (1979) considered that the origin time of the glyptosternoid fishes may be later than that geological time, it is most possible in the later Pliocene. Firstly, in the South-Eastern Tibet, the *Glyptosternum*-like species originated. We can choose the out-group in the family Sisoridae from all the groups outside the glyptosternoid fishes, but, based on the narration above, I consider that the *Bagarius* and *Glyptothorax* are more suitable to be the out-group. At the structure of the skeleton, they are very similar, and the *Glyptothorax* has more wide distribution. Outside the glyptosternoid fishes, in Sisoridae, there exist 11 genera: they are *Glyptothorax*, *Bagarius*, *Gagata* and *Pseudecheneis*, and only in Indian, *Conta*, *Pseudolaguvia*, *Erethistes*, *Erethistoides*, *Nangra*, *Sisor*, *Hara* and *Laguvia*. Either on the morphological or the osteological characters (e.g., Tilak, 1963b; Gauba 1967), *Bagarius* and *Glyptothorax* are the most primitive. The Diplomystidae have been traditionally regarded as the most primitive taxon of the Siluroidei (Regan, 1911; Alexander, 1965; Chardon, 1968; Lundberg and Baskin, 1969; Fink and Fink, 1981), so Diplomystidae are treated as a reference for deciding the evolutionary polarity.

The concept of the glyptosternoid fishes first comes from the genus *Glyptosternum*. In 1922, Hora restricted the use of the generic name *Glyptosternum* McClelland to the species in which "the first ray of the pectoral and ventral fins soft and pinnate, giving off soft pointed cartilaginous rays along the anterior margin, which are enveloped in the membrane of the fin", in that time, the glyptosternoid fishes only included *Glyptosternum*; in 1952, Hora revised the glyptosternoid fishes and arranged the other fishes that own similar pectoral ray in this group; also, the earliest *Glyptosternum* was separated in several genera; so there were 7 genera and 19 species arranged in this group. Until now, in this group, there are 9 genera and 31 species.

In the character analysis and the cladogram, except the pectoral fin ray, there are many characters to define this group: **1**. The posterior tip of the lateral ethmoid prolonged and extended out the margin to form a remarkable protrusion; **2**. The anterior part of the frontal is very narrow, the width is far smaller than that of the posterior part; **3**. A prominent ridge formed wholly by dentary, most length of the lower jaw is formed by the dentary; **4**. The palatine is enormously developed, broad, strong and spatulated at both ends, articulating with ectethmoid by its center; posteriorly encloses a cup shaped space; **5**. The ectopterygoid is smaller than the metapterygoid, and connected with the metapterygoid only by its thin posterior end; **6**. The interoperculum is thin and long, it is as long as the length from the anterior tip of the dentary to its posterior end; **7**. The opercular is quadrilateral; **8**. The 5th parapophysis is undeveloped, it is far shorter than the 4th parapophysis; **9**. The posttemporal is an unbranched bony plate, without the inferolateral limb, the anterior margin of the gasbladder capsule is contacted to the exoccipital; **10**. The last unbranched pectoral fin ray is soft and giving off many point soft protrusions along its anterior margin; **11**. The pectoral girdle, the posterior dorsal margin

forms an acute angle with its anterior margin, the antero-medial part formed by cleithrum and the coracoid is not very wide; 12. On the anterior margin of the 2nd dorsal fin ray, it gives off many feather-like point soft protrusion, this character is similar to what on the pectoral fin; 13. The dorsal neural spinal of the 4th vertebra is undeveloped, plate-like, unbranched, and is not connected to the proximal radial of the dorsal fin; there is not distinction between neural spinal 4th and the bony ridge of the skull.

From these definite characters, it is apparent that this group is a monophyletic group. And it is possible that they developed under the strong stress of the torrential environment, because all the species have a very depressed body, and own the different attaching organs; also its recording of the distribution are mountain brooks, or the rivers around the hills. Its appearance, most probably is due to the successive orogenic movement in Pleistocene.

About its systematic relationships, most of the studies before were based on the description of the adaptive characters (Hora, 1952; Chu, 1979). The common point of the present work with them is that *Glyptosternum* seems to be the most primitive species. Actually, this species shows a wide geographical distribution. But by the concept of the parsimony, some of the adaptive characters, which were used before as the systematic characters, here are treated as a convergence, such as a mouth sucker, post-labial fold, the maxillary barbels, the maxillary and dentary teeth, etc. The most problem conflict is the mouth sucker and the post-labial fold: in *Exostoma*, *Oreoglanis*, *Pseudexostoma*, and *Myseriglanis*, there is a complete mouth sucker with a continuous post-labial fold. This made some authors consider they are descended from a same ancestor. But a very important character in a very long time, had not been mentioned in *Glaridoglanis*, *Pareuchiloglanis feae*, *P. kamengensis*, and *P. gongshanensis* until Chu's (1992) paper; in these genera and species, a complete mouth sucker lacking, the post-labial fold is not continuous, but the post-labium is very developed. Between the labium and the maxilla, there existed a groove which makes the post-labium free, actually this is a kind of primitive mouth sucker. From the character analysis above, it is easy to consider that the mouth sucker of *Pseudexostoma*, and *Origlanis* has developed from *Pareuchiloglanis feae*, *P. kamengensis*, and *P. gongshanensis*; also, the mouth suckers in *Exostoma* and *Glaridoglanis* a have systematic relationship.

In the cladogram, the genus *Pareuchiloglanis* is not a monophyletic group; it forms a monophly only when *Pseudexostoma* and *Oreiglanis* are added in, may be, *Myseriglanis* and *Parachiloglanis* must be included. Actually, the genus *Pseudexostoma* and *Oreiglanis* are two specialized species in *Pareuchiloglanis*. The sister group, *Exostoma* and *Glaridoglanis*, descended from *Euchiloglanis*, and forms a sister group with *Pareuchiloglanis*, *Pseudexostoma* and *Oreiglanis*. Although bearing some prominent specialized characters (teeth, mouth sucker, etc.), it owns more primitive characters: branched pectoral fin rays are 10-12; gill opening is middle; thin and sharp maxilla barbels; also some osteologic characters. *Euchiloglanis*, only distributed in Jinshajiang river and its tributaries, is a relatively primitive genus. It bears remarkable primitive characters: the premaxilla stretched posteriorly and composed by three parts. The cladogram shows that it is derived directly from *Glyptosternum*.

Conspicuously the evolutionary tree of the cladistics of this group is not in complete correspondence to what in the traditional taxonomy. How to resolve this conflict, need to be discussed deeply next.

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APPENDIX: ABBREVIATIONS

af = anterior fontanelle;	alp = anterolateral process;	
amp = anteromedian process;	anh = anterohyal;	ap = anterior process;
ar = arch;	ars = articular surface;	art = articular;
bah = basibranchials;	bfr = branched fin ray;	bo = basioccipital;
brst = branchiostegal ray = lepidotrichia;		
C5 = 5th centrum;	cap = capsule for gasbladder;	
cc = complex centrum;	cd = coracoid;	ceb = ceratobranchials;
cn = centrum;	cr = complex radial;	ct = cleithrum;
cuc = compound ural centrum;		
den = dentary;	doh = dorsohyal;	
dpc = posterior part of the dorsal process of cleithrum;		dr = distal radial;
dsp = dorsal spine;		
ect = ectopterygoid;	ep = epural;	epb = epibranchials;
epo = epiotic;	eth = ethmoid;	exo = exoccipital;
f = fenestra;	fr = frontal;	
hcp = humero-cubital process;	hpu2 = haemal spine of preural centrum 2;	
hu = hypurals;	hyb = hypobranchials;	hym = hyomandibular;
iop = interopercular;	ipot = inferior limb of posttemporal;	
lac = lachrymal;	leth = lateral ethmoid;	lp = lateral process;
max = maxilla;	met = metapterygoid;	mf = foramen magnum;
ns = neural spine;		
op = opercular;	ors = orbitosphenoid;	
P5 = 5th parapophysis;	pal = palatine;	pap = parapophysis;
pbh = pharyngobranchials;	pf = posterior fontanelle;	ph = parhypural;
pha = post-haemapophysis;	pmx = premaxilla;	poh = posterohyal;
pop = preopercular;	pot = posttemporal;	pp = posterior process;
ppt = primary pterygials;	pr1-2 = proximal radials;	pro = prootic;
ps = pectoral spine;	psh = parasphenoid;	pto = pterotic;
pts = pterosphenoid;	pu = preural centrum;	
q = quadrate;		
r = rib;		
sph = sphenotic;	spt = secondary pterygials;	suo = supraoccipital;
un = uroneural;	urh = urohyal;	
v = vertebra;	veh = ventrohyal;	vo = vomer;
vp = ventral process.		